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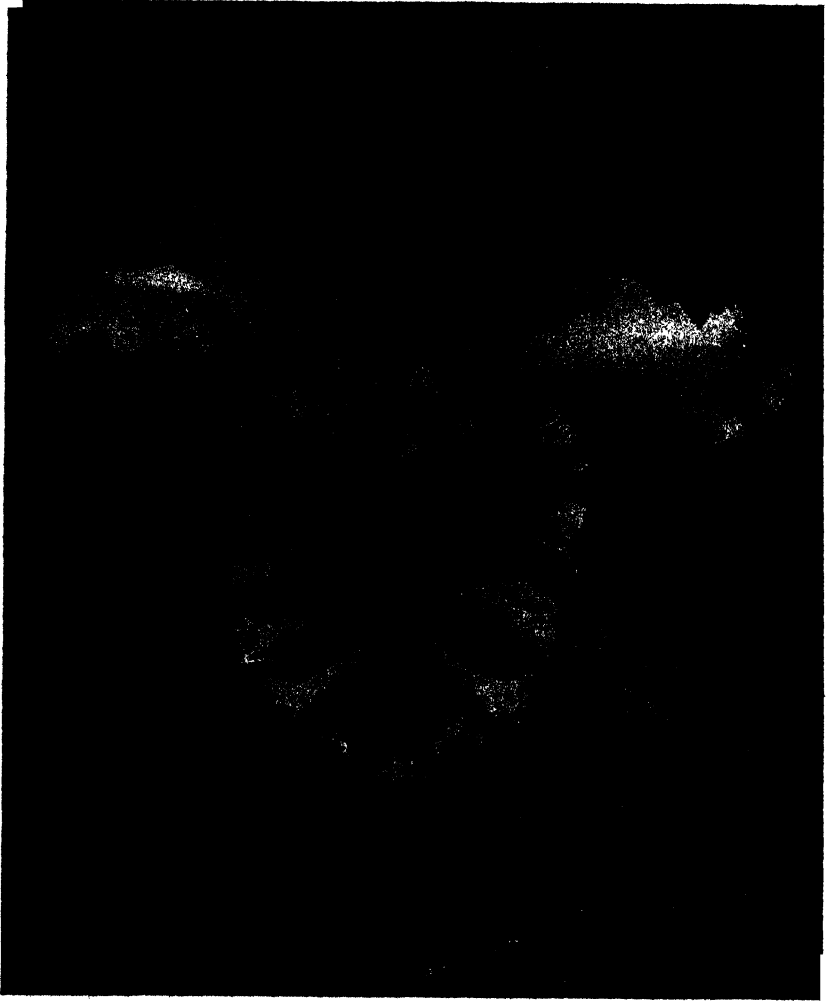
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The bilaterally symmetrical flowers of orchids are among the most highly specialized of the monocotyledons. Pictured here is a representative of the large orchid genus *Cattleya*.

THE PLANT WORLD

A Text in College Botany

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DEDICATED

TO THE MEMORY OF

MY MOTHER AND FATHER

Preface

This textbook is intended primarily for use by students who are registered in elementary botany courses principally because of the cultural and general educational value of the subject rather than because of its usefulness as a prerequisite to a professional botanical career. Courses of this general educational nature frequently contain a heterogeneous population of students majoring in history, languages, commerce, law, sociology, agriculture and other fields. The heterogeneity of interests and of previous experiences embodied in such a group constitutes a serious teaching problem, for the instructor must first arouse interest among a considerable portion of his students before he can hope to instruct them in the biology of plants. The author believes that, in order to create and sustain such interest, an instructor must associate the study of plants, insofar as it is possible, with the everyday experiences of his students and emphasize particularly those botanical principles which are illustrated in such phenomena as plant growth, flowering, seed production and germination, soil fertility, nature cycles, economic uses of plant products, etc.

The author believes that the primary objective of an elementary botany course, designed for the needs of general education, should be the presentation of the fundamental features of the structure, physiological activities, and reproduction of flowering plants. Secondary objectives should be, first, to emphasize those aspects of plant life which are important in the great cycles of nature and which are directly or indirectly concerned with human living; second, to give students a panorama of the kinds of plants which now inhabit the earth and of the major features of their behavior; and third, if the course is of sufficient length, to present a brief, generalized account of plant evolution.

In accordance with his convictions concerning the importance of these objectives, the author believes that there is little justification for the inclusion, in a course based upon these objectives, of such subjects as the study of the origin and evolution of heterospory in plants, of the

details of reproductive processes in club-mosses, horse-tails, cycads and other minor groups, of the minutiae of tissue-system development from meristems, of the prolonged and prayerful consideration of life-histories from *Oscillatoria* through *Pinus*, etc. These subjects accordingly have received only brief attention or have been omitted.

The book is arranged in such fashion that Parts I, II, and III may be used as reading material in brief courses in botany. For longer courses, the topics on evolution and ecology, treated in Part IV, may be conveniently added to the required reading of the first three sections.

The author wishes to express his deep gratitude to Dr. Charles F. Hottes, Dr. Oswald Tippo, Dr. Neil Stevens, Dr. J. T. Buchholz, and Dr. Arthur B. Cozzens for their critical reading of portions of the manuscript and for their helpful suggestions. The author wishes further to acknowledge his indebtedness to the following persons and institutions who have made available numerous excellent photographs for inclusion in this book: Dr. Charles F. Hottes, Dr. George T. Moore and the Missouri Botanical Garden, the Field Museum of Natural History, the General Biological Supply House, Dr. George Conant and the Triarch Botanical Products Company, the U. S. Forest Products Laboratory, Dr. Harry Andrews, Dr. Benjamin Koehler, Dr. Oswald Tippo, Dr. O. T. Bonnett, Dr. A. G. Vestal, Dr. V. E. Shelford, the University of Illinois College of Agriculture, Dr. W. A. Ruth, Dr. W. C. Steere and Dr. E. B. Mains, the Armstrong Cork Company, Dr. A. B. Cozzens, Dr. C. J. Alexopoulos, and Dr. J. M. Schopf and the Illinois State Geological Survey.

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Part III: The Plant Kingdom

PART I

The Nature of Plants and
of Plant Study

Plant Study: History, Development, and Importance

1. ORIGIN AND HISTORY OF BOTANICAL STUDY

THE SERIOUS study of plants arose probably in the efforts of early man to control and utilize his vegetational environment as a source of food, shelter, clothing and fuel. If this intensely utilitarian exploitation of plant forms, products, and behavior constitutes a field of botany, then we might say that botany had its beginnings in the stage of man's evolution at which he became able to entertain more than one idea at a time and to react with the maximum degree of personal advantage to his natural environment. So we may say that *Pithecanthropus erectus*, the Java ape-man, was something of a botanist and that certainly his later relatives in the family tree of man, the Neanderthal man, the Cro-Magnon man and others were practical botanists of at least a sufficient degree of success to enable them to survive.

Most plant scientists of the present day, however, would be unwilling to consider these early men botanists or to elevate their trial and error methods of utilizing plant power to the rank of the science of botany. To most practitioners of science, science begins only when facts are intelligently and logically organized, and when, on the basis of this organization, accurate prediction becomes possible.

On the basis of this interpretation of science as the dispassionate collection and evaluation of knowledge, aside from any immediate utilitarian demands, botanists usually recognize the beginnings of plant science in the Golden Age of Greece. In Greece, as in other countries, the study of plants at first began with practical aspects — the uses of plants as food for men and animals and as sources of medicinal drugs. Along with the study of these there developed slowly the study of plants for their intrinsic interesting features of structure and behavior.

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Most of the early Greek botanists were physicians or drug sellers, who, as they studied the healing properties of plants, made studies of variations in plant forms, of apparent relationships among plants, and of agricultural practices.

Outstanding among these Greek botanists was Theophrastus, a pupil of Plato and Aristotle, about 340 B.C., who wrote a *History of Plants* in which he described the forms, behavior, and properties of some five hundred food and medicinal plants. Theophrastus' book deals in considerable detail with the general morphology of roots, stems, leaves, flowers and fruits of plants and refers to such anatomical features as fibers, vessels, wood, bark and pith. The uses of wood for timber, diseases of trees and shrubs, dispersal of seeds, exudation of resins from coniferous trees, conditions necessary for the development of fig and date fruits, uses of ornamental plants, and importance of vegetables and cereals are other subjects given emphasis in the *History of Plants*. A second work of Theophrastus, *The Causes of Plants*, discusses seeds, grafting methods, the effects of temperature extremes upon plants, the relation of weather to soils, agricultural practices in plant cultivation, the death of plants, the perfumes and tastes of plants, and numerous other botanical topics.

Aristotle wrote of plants in a more general fashion, chiefly from the standpoint of their philosophical aspects. Aristotle wrote that plant life is lower and less specialized than animal life, citing as evidence the fact that several parts of plants grow easily into new individuals, whereas separated parts of animal bodies are incapable of such regeneration. Aristotle believed also that plants had no sensory faculties, that they had no differences of sex, and that the roots of plants were feeding organs similar in function to the mouths of animals. He reached the unique conclusion that animals have souls and plants do not!

Rome, too, contributed to the science of plants, but her efforts were trivial as compared with those of the Greeks. Doubtless the outstanding of Rome's botanists was Pliny, the Elder, who early in the first century A.D. described almost a thousand species of plants, most of which were highly valued for their medicinal uses. Pliny's *Natural History* contained so many errors that it has been called "a repository for all the errors of antiquity." Thus it can scarcely be regarded as an important work in the history of botanical study. Another Roman student of plants was Dioscorides, who early in the Christian era wrote a valuable book on medicinal plants. This manuscript was primarily a compendium of information about the medical uses of plants, though it contained in

Fig. 1. An illustration of a mandrake plant, from an old herbal.

addition some rather advanced views concerning the relationships of several plant groups, particularly the mints, legumes, and composites.

The Middle Ages constituted a period of relative inactivity in European science as a result of the vast political and cultural changes which followed the decline of the Roman Empire. The study of biology particularly was hampered by the Church's insistence upon adherence to the Aristotelian principles of philosophic science. Biology became a study of tradition and as such made little progress, for experimentation as a technique of knowledge was discouraged. During the medieval period, particularly between 800 A.D. and 1300 A.D., there was considerable scientific activity among the Arabians. Much of the botanical interest in Arabia centered upon the medicinal properties of plants. Botanical gardens were established in various parts of the Arabian empire and there developed considerable traffic in seeds and plants among these institutions. Baghdad became a center of the translation and editing of early Roman and Greek botanical manuscripts into Arabic. Though this scientific activity was energetic and extensive, it could scarcely be termed original or progressive, for Arabian scientists venerated the works of Aristotle and employed them as the guiding principles in their investigations, attempting to force their observations into the patterns formulated by Aristotle. Hence, not until ten centuries after the fall of the Roman empire, with the inception of the Renaissance, did the experimental study of plants resume the course that the Greeks had begun to map out for it.

During the sixteenth century botanical gardens became popular and by the middle of the seventeenth century there was hardly a university or a medical school in Europe without a garden of medicinal herbs and shrubs. The study of plants during this period continued to center about their utilization as sources of drugs and food plants, an emphasis which is strongly reflected in the Herbals, ponderous tomes written in the sixteenth and seventeenth centuries and containing descriptions of medicinal and food plants, drawings from living plants and copies of earlier plates and frequently impassioned discourses on theology, pedagogy and peculiar natural phenomena which we now know to have been myths and superstitions. Among the outstanding authors of these books were Otto Brunfels, Leonard Fuchs, famous for his excellent woodcuts, and Hieronymus Bock, who emphasized the importance of description of plants in their natural, living condition. One of the most prolific of these herbalists was Gaspard Bauhin, who in 1623 published excellent descriptions of nearly 6,000 species of plants and whose work

Portraict de l'Arbre qui porte des fueilles, lefquelles tombées fur ter-
re fe tournent en oyfeaux volants, & celles qui tombent dans
les eaux fe muent en poiffons.

Fig. 2 An illustration from an old herbal of a tree, the leaves of which, falling
upon the soil, turn into birds, and falling into the water, become fish.

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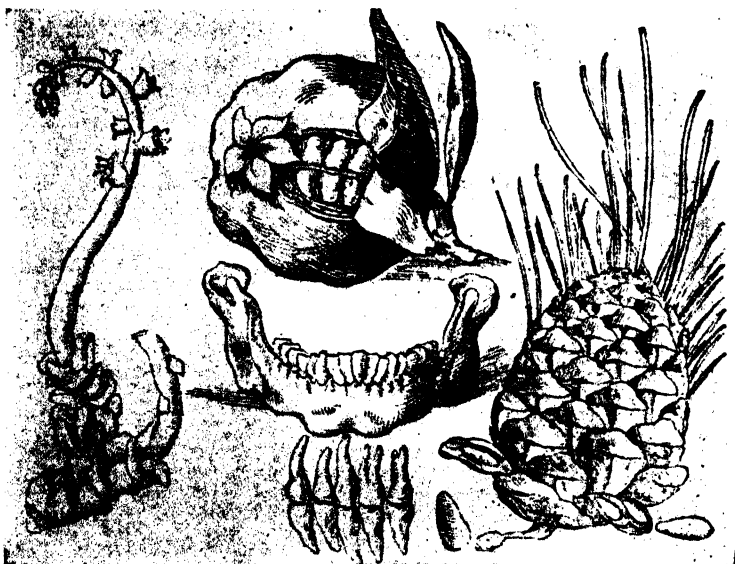
Fig. 3. An illustration from an old herbal, illustrating the Doctrine of Signatures. Note the resemblance between the human teeth and the cone scales of pine and pomegranate seeds.

is still used today in the study of the original characterizations of many important plant species.

Many fantastic drawings (Figures 1, 2, 3, 4) appeared in these Herbals and with them many bizarre stories and descriptions, included as undoubted scientific facts. A cycle of legends and beliefs developed around the so-called "Doctrine of Signatures," one of the principal supporters of which was Paracelsus who lived during the sixteenth century. According to this doctrine, certain plant organs were modelled upon structural principles similar to those of human organs; these plant organs supposedly constituted more or less specific remedies for diseases of the human organ which they most closely resembled. Hence, the sap of the blood-root was administered as a blood tonic in anaemia, the porous leaves of the St. John's-wort were used in treating holes or cuts in the skin, the walnut with its numerous invaginations and convolutions was employed extensively in brain diseases, and so on. Some of these early scientists were not without a certain sense of the occasional inaccuracy of their theories; one of them humorously confessed, "most of these I am confident are true, and if there be any that are not so, yet they are very pleasant."

are essential for the existence of all animal life. All of the food we eat comes directly from plants or indirectly, in the form of meat, fish, eggs, and other animal products, which were formed at the expense of plant tissues eaten by these animals. Further, we are indebted to plants for the other necessities of our existence — fibers for clothing, lumber for shelter, drugs for our ills, and for the many luxuries which add comfort and delight to life — spices, perfumes, beverages, dyes, coal, paper, and other cellulose products, rubber tires for our automobiles, lubricants, paints, lacquers, and dozens of other products of plant activities. The tremendous indebtedness of mankind to plants is sufficient reason in itself to justify the study of plants. In such study, the student comes to realize the magnitude of his indebtedness and the significance of plants in the scheme of nature, to appreciate the intricacies and ceaseless activities of plants, and thus in part to discharge his indebtedness.

In the second place, a liberal and balanced education is enriched by a study of plants. Education is frequently defined in terms of its desired result: the most satisfying and most advantageous adjustment to one's environment. If this is true, then the study of plants is an essential feature of effective education; for in man's environment there are two dominant, omnipresent entities — the green vegetational cover of the earth, and the sky. The appreciation of artistic and literary works is frequently enhanced by some acquaintance with living plants.

In the third place, there are philosophical rewards in the study of plants. The appreciation of the beauties of flowers, of forests, and all other aspects of plant life is sharpened, and amplified by a knowledge of the myriad activities which transpire behind the stage of nature and which are apparent only to those who seek them out. Further, the realization of the unifying principles of plant and animal development and behavior, the awareness of the order and magnificent design underlying the growth and structure of plants and the discovery of the sensitive balances and counterbalances regulating the lives of all organisms, contribute to the unfolding of a sane and appreciative philosophy of life and of man's place in nature's economy.

Finally, of course, students planning to embark upon professional careers in applied plant sciences — horticulture, agronomy, plant breeding, forestry, plant disease control, and soil conservation, and likewise students of pharmacology, require botanical knowledge as a fundamental tool. Even in fields less directly related to botany, such as bacteriology, the practice of medicine, and public health service, a knowledge of botanical principles is often equally profitable.

SUMMARY

1. Botany is the science of plant life.

2. Scientific botany in the Western world had its beginnings in Ancient Greece. Several Greek and Roman scientists, particularly the former, made fundamental observations upon plants. Foremost of these Greek investigators was Theophrastus (about 340 B.C.). All were interested especially in the medicinal and agricultural aspects of plant life.

3. During the Middle Ages, there was relatively little progress in the scientific study of plants. Most of the botanical work of this period involved mixtures of superstition and mythology with botanical facts. The chief botanical books of the Middle Ages were called "Herbals."

4. The modern period of scientific botanical study began in the latter part of the seventeenth century.

5. The major fields of modern botany are:

    a. plant taxonomy — the study of plant classification, identification, and relationships.

    b. plant morphology — the study of plant structure.

    c. plant anatomy — a phase of morphology, emphasizing the microscopic structure of plants.

    d. plant physiology — the study of the functions and activities of plants.

    e. plant pathology — the study of plant diseases.

    f. plant genetics — the study of inheritance and breeding.

    g. plant ecology — the study of relations between plants and their environments.

    h. plant cytology — the study of cell structure and behavior.

6. Applied fields of plant science closely related to botany are:

    a. floriculture — the study of ornamental plants.

    b. agronomy — the study of crop-production.

    c. pomology — the study of fruit-production.

    d. olericulture — the study of vegetable crops.

    e. bacteriology — the study of bacteria.

7. The word "botany" may be traced back through a series of Greek words meaning "plant" and "graze" to the Greek word for "cattle."

8. The study of botany is valuable for these reasons:

    a. It enables man to appreciate his dependence upon plants and his place in nature.

    b. It enriches the cultured life and enhances the esthetic appreciation of plants by educated people.

    c. It forms a necessary informational background for students preparing for careers in horticulture, agronomy, bacteriology, forestry, pharmacology, soil conservation, etc.

The Manifestations of Life; Plants and Animals

1. THE NATURE OF LIFE

IN THE study of a science, one must determine a few fixed points as sources of reference and comparison for the interpretation and evaluation of newly acquired knowledge. Since many of the phenomena of nature seem to be more or less continually in a state of flux and change, these points of reference vary from time to time; they are only relatively fixed and they shift as new discoveries demand their alterations. In our study of botany we must begin with two apparently fixed points — an understanding of the significance involved in the word "life" and a fairly clear idea of the meaning of "plant." Because of numerous exceptions to rules and the inadequacy of words to express such complexities, we are able to define these ideas adequately only in terms of the phenomena which they exhibit.

Any attempt to define "life" directly leaves us struggling incoherently for words. We can say that life is an organization of activities manifested by living beings and then proceed to describe these activities which are more or less peculiar to the living state.

The more obvious indicators of life — movement, growth, reproduction — are not valid criteria of life without more specific definition, since they also characterize non-living entities in some degree; rivers grow, produce new rivers, stalactites grow, a bit of camphor on the surface of water moves swiftly to and fro, but they are not alive. If we examine more carefully and more deeply into the phenomena of life processes, we can qualify these obvious indicators and specify at least five characteristics which seem peculiar to living things:

1. The power of **assimilation** of non-living materials; that is, the capacity inherent in living matter of modifying alien substances and transforming them into the very living substance which brings about

their alteration. Examples of this phenomenon may be found wherever the intake, digestion and assimilation of food occur — the transformation by man of the foods he ingests into blood, muscle, bone, hair, etc., the synthesis by plants of sugars from carbon dioxide and water (**photosynthesis**) and the subsequent transformation of some of these sugars and other substances into the proteinaceous living substance, **protoplasm**. Assimilation is a fundamental feature of **growth**.

2. The quality of **irritability**, involving the sensitivity of protoplasm to changes in the environment and the capacity of specific reaction to those changes. Protoplasm is sensitive to a wide variety of the external features of its environment — to light, variations of temperature, moisture and drought, wounding, mechanical stimuli, such as pressure, tension, etc., chemicals, gravity, etc. The reactions of protoplasm to these changing factors possess survival value, for the reactions tend usually to adjust the organism more or less favorably with reference to the particular stimuli involved. As evidences of the advantageous nature of these reactions, one may mention the movement of the leaves and stems, the food factories of the plant, toward light, which supplies the energy for food synthesis, the avoidance of hot stoves by children who have been burned, and the bending upward toward air and light of stems of plants which have been beaten down by wind and rain. In considering this probable survival value of reactions to stimuli, one must carefully avoid assuming any conscious, premeditatedly advantageous response of plants and the lower animals to stimuli. Rather than adopt the view that such organisms react consciously or purposefully, that they react as they do because they wish to survive, we should say that they survive because they are able to react; that is, because protoplasm by virtue of its structure and organization possesses the inherent powers of sensitivity to, and of reaction toward stimuli. The reactions of living organisms to stimuli consist chiefly of movements of the whole organism or its parts with reference to the exciting stimuli.

3. The power of **reproduction** of similar kind, the transmission from one generation to the next of similar structure and behavior characteristics. It is the obvious, the commonplace, which we take for granted and for which we rarely ask an explanation; we are so well acquainted with the fact that cats never give birth to oysters and that rosebushes never grow from bean seeds, that we often neglect to include this particular feature of protoplasmic behavior among the criteria of life. It is one of the most fundamental of these criteria and one of the most universally apparent; not only does a species produce offspring of the

same species, but the offspring usually resemble in a high degree their parents; that is, the individuality within a species tends to be transmitted from parent to offspring.

4. The power of decomposing certain organic substances called **foods** with the release of energy which makes possible the operations of life — movement, growth, digestion, reproduction, etc. This process of energy-release is known as **respiration** and is peculiar to living matter. The foods most commonly involved in respiration are certain simple sugars, although other substances such as ammonia, nitrites, organic acids, proteins, etc., may also be respired. Their decomposition in respiration forms the almost universal source of energy for the physiologic processes of organisms, with the exception of **photosynthesis** which depends upon sunlight for its energy. Photosynthesis is the fundamental process of food manufacture in green plants; it transforms the energy of sunlight into the stored energy of foods, energy which is then made available for vital processes by respiration.

5. Living organisms possess a characteristic type of structure which distinguishes them from non-living things. The bodies of plants and animals are composed of microscopic structures called **cells**, each of which consists of a tiny bit of living substance, or **protoplasm**, and an enclosing wall or membrane. The cellular plan of organization is an exclusive property of plant and animal bodies.

Thus we see that life is a flexible, plastic phenomenon. It involves numerous processes of chemical and physical change, of growth, of movement and reactions to stimuli, of food-getting and assimilation, of obtaining energy, of reproducing and propagating the species. It seems possible that these characteristics of living things are explainable in large degree in terms of less complex chemical and physical processes which are constantly ebbing and flowing in protoplasm. It is a fact that all of the chemical elements which are found in living protoplasm occur likewise in the non-living materials of soil, rocks, air, and water. Thus, there is no single chemical element which is peculiar to living matter. The secret of life lies not in the nature of the ultimate substances of which protoplasm is composed, but rather in the organization of these chemical elements into a living system. The example of a watch, broken, then repaired, is frequently used to illustrate this point. The watch in its broken, useless state contains exactly the same kinds and quantities of constituent materials as it does when it is repaired, but the repaired watch possesses an organization which makes it a useful functional instrument, not merely a mass of inert metal and glass.

2. THE EXPLANATION OF LIFE

The question as to whether or not the intricate phenomena of life are in the final analysis explainable in terms of physical and chemical reactions has produced two schools of scientific thought, those of **vitalism** and **mechanism**. These two attempts at an explanation for the living condition are not sharply defined; there are various theories of mechanism and several of vitalism; some are sharply opposed, others are more diffuse in their contentions and may even coincide at certain points. They may, however, be considered as two rather strongly opposed attempts to explain the nature of life.

According to the vitalistic idea, there is present in living organisms a vital essence, or force, which is peculiar to living organisms and which is different from all other forces found outside of living things. This vital force, which is the driving power of the living condition, is not explainable in terms of physico-chemical phenomena. Death ensues when this force is destroyed or leaves the organism. We cannot study or analyze this vital spark, according to the adherents of this theory, because it resembles no other force in existence and by its very nature it is beyond man's analysis and understanding. Vitalism, then, insists that the differences between living matter and non-living substances are primarily qualitative, that is, differences of kind rather than of degree.

The philosophy of mechanism holds that there is no mysterious force especially characteristic of living beings, but that all life processes can be interpreted by the application of chemical and physical laws. In other words, the differences between living protoplasm and non-living chemical compounds are largely quantitative differences, differences of degree rather than of quality. Mechanists believe that the existence of unexplained processes and reactions of living organisms does not imply the presence of immeasurable vital forces, but rather that at the present time, scientific methods and technique are still too clumsy and inadequate to analyze such complex phenomena. With the advance in man's mental powers and scientific dexterity through future decades, they believe that these at present unexplained life phenomena will yield to interpretation by the application of chemical, physical, and mathematical laws.

The idea of vitalism arose at a time when most of the activities of living organisms seemed mysterious and inexplicable. As scientific discovery progressed, however, the vitalistic interpretation suffered re-

peated damaging assaults. Phenomena which seemed impossible of explanation to older generations of scientists were shown one by one to be amenable to quantitative physico-chemical explanations. This energetic attack upon the stronghold of vitalism achieved its greatest success in the latter part of the nineteenth and the beginning of the twentieth century, a time during which chemical and physical science made phenomenal advances and thus gave new weapons to mechanistic biologists. During this period vitalism lost prestige and became almost extinct as a biological philosophy, as more and more vital phenomena were proved to be of chemical and physical nature.

At the present time there seems to be among certain biologists a re-awakened interest in the vitalistic philosophy. These biologists believe that, although many processes in living organisms have been explained mechanistically, there remain other phenomena which have resisted attempts at physico-chemical interpretation. The complexities involved in the powers of adaptation of living organisms to changing environ-mental factors, in the intricacies of the absorption and secretion of materials by living cells, in the formation of habits both in plants and animals, in the delicate interrelations between many kinds of flowers and the insects which pollinate them, in the phenomenon of variation, and in certain phases of inheritance seem to these biologists to differ from the phenomena of the inanimate world in quality as well as in degree. And it seems not unreasonable to these neo-vitalists to assume that these are vital phenomena for which we have no scientific yard-stick, and which we cannot duplicate in the test tube nor explain by the same methods of analysis which we apply to the behavior of non-living matter.

The biologists who subscribe completely to the mechanistic philos-ophy as a working tool have vigorously defended their methods of investigation. They maintain that the essential question involved in the argument between the two philosophies is whether or not a solution of any of the problems of living organisms has ever been achieved *outside* of the mechanistic technique, *not* whether an explanation of the nature of life can be found *within* the mechanistic approach. The obvious answer to the first question favors the mechanists; all of the funda-mental explanations of living processes and structures thus far devised have resulted from the application to living organisms of the same assumption and skills employed in the physical sciences. To the second question, the mechanists answer that there is no justification for a dog-matic statement that they believe all properties of living organisms will

eventually be reduced to physico-chemical interpretations. They assert merely that since the mechanistic method of study in biology has been so productive in the past, it should be retained as a future technique, regardless of its eventual usefulness in explaining the ultimate nature of living processes. The mechanistic philosophy, its adherents believe, stimulates interest in the investigation and solution of biological problems, whereas the vitalists' approach is likely to develop a less aggressive attitude toward such problems and a feeling of complacency in the face of the present limitations and failures of human effort.

Though it may seem anomalous, it is possible for biologists to appreciate the significance of both philosophies. So long as our scientific methods are based upon objective experimentation and upon adherence to the law of cause and effect, it is logical that, whenever it is possible, our investigations should be based upon the mechanistic philosophy. However, we should be cognizant at all times that some of the phenomena with which we deal may be of a different type from those readily amenable to objective physico-chemical explanations. An awareness of the intricacy and complexity of life may save the biologist from making embarrassing errors which might arise from dogmatic assertions that all vital activities can be explained mechanistically, and also opens a path to further philosophical inquiries, a path barred as effectively by an obdurate mechanistic philosophy, as by a resigned and complacent vitalistic outlook.

3. ORIGIN OF LIFE

' The problem of the manner in which life originated on the earth has always puzzled biologists and apparently will continue to do so well into the future, perhaps for all time. All that we know is that living protoplasm existed on the earth eons ago, that it probably originated in the oceans which covered most of the earth's surface, and that it was extremely simple structurally, possibly very similar in its minuteness and morphologic simplicity to some of the organisms — pond-scums, bacteria, etc. — which are dwelling upon the earth today. We do not know by what action or series of actions the first bits of protoplasm were formed. Many biologists in the past have subscribed to the theory of **spontaneous generation,** which holds that living protoplasm develops directly from non-living matter. The work of numerous biologists, including Pasteur, proved definitely that the living protoplasm which they studied developed from pre-existing protoplasm. The supporters

of the spontaneous generation theory based their contention upon such evidence as the appearance of bacteria in broth or in decomposing meat. Pasteur and others showed that, if the meat and broth were heated for a time and protected from air currents, no bacteria developed. Bacteria are present in air and, when they fall into such organic materials as these, they grow and reproduce. Thus occurs the multiplication of these living organisms, as offspring of parent organisms, not as transmutations of the non-living organic materials present in meat and broth. Although modern biologists generally consider the theory of spontaneous generation disproved, this belief in its old form frequently crops up in the hinterland. One occasionally hears reports of horse-hairs turning into worms in water-troughs, and of maggots forming from dead flesh. Such accounts usually originate from superstitious people of no education and of limited powers of observation. The generally accepted belief at present, then, is that living organisms develop only as offspring of other living beings, never as products of non-living substances.

Some biologists regard **filterable viruses** as entities possibly intermediate between living and non-living matter. The filterable viruses, so-called because of their ability to pass through filters which restrain all known living cells, cause many diseases (e.g., tobacco mosaic, peach yellows, and tomato mosaic) of higher plants and of higher animals (e.g., infantile paralysis, herpes, or fever-sores, smallpox, and measles). Viruses seem to have one property in common with living organisms — namely, the ability to reproduce or to increase themselves. Since the virus particles are too small to be visible under a microscope and since they do not possess other characteristic qualities of life they cannot reasonably be admitted to the company of living things. Many biologists regard them as having little bearing upon the problem of life's origin and reaffirm their belief in the Biogenetic Hypothesis — namely, that all living protoplasm originates only from other living protoplasm.

Another theory concerning the origin of life is one which holds that life on our planet came to us from some other world, possibly from one of the other members of our solar system. This idea has at times had a considerable following among scientists. In the absence of credible evidence in its support it has but few adherents at the present time.

Some people assume, entirely as a matter of faith, a Divine Creation of living substance. The only alternative seems to be the assumption that at some time in the dim past, the chance association of the requisite chemicals in the presence of favorable temperature, moisture, etc.,

produced living protoplasm. In other words, if one subscribes to this theory, he admits that the first protoplasm to appear on our earth was a product of spontaneous generation. Then, if he accepts the evidence of Pasteur and others against spontaneous generation, he must reverse his explanation of the origin of the *first* protoplasm to explain the origin of all subsequent living protoplasm from that first protoplast. In other words, spontaneous generation, according to these opponents of the idea of Divine Creation, worked when the first living substance was formed, but probably hasn't worked since. Actually, biologists are still as far away as they ever were in their attempts to explain how the first protoplasm originated. The evidence of those who would explain life's origin on the basis of the accidental combination of suitable chemical elements is no more tangible than that of those people who place their faith in Divine Creation as the explanation of the development of life. Obviously, the latter have as much justification for their belief as do the former. It is possible that the problem of life's beginning on our planet will always remain insoluble, a philosophical question rather than a subject capable of experimental investigation and solution.

With the passage of centuries, ceaseless changes occurred in the topography, the climate, and the plan of the earth's surface, and the progeny of the first bits of life, whatever their origin, gradually became transformed into different types of organisms, possibly in part as adaptations to changing environmental conditions, partly in response to internal genetic factors. In other words the processes of evolution were at work and are still at work today, molding, eliminating, changing, adding to the various forms of life which live on the earth's surface.

4. PLANTS AND ANIMALS

At some time in the course of evolution the differentiation of organisms into plants and animals occurred. Such modifications, we must remember, probably did not occur at a single instant in evolutionary history, but very likely arose here and there, under different conditions, at different periods. We cannot logically say that the plant kingdom originated from the animal, or the animal kingdom from the plant, although it seems probable that earth's first organisms were capable of synthesizing complex organic compounds from the simple, inorganic substances of air and soil, a process which is characteristic of plants rather than animals. It seems that here and there in the course of evolution, some organisms assumed plant-like features in varying de-

grees, others became animal-like. These changes occurred at different times; some persisted and the differences which they produced became intensified, others weakened and died out. We may think of the whole course of the evolution of living creatures in terms of a tree, with its roots below ground hidden from our eyes, with new twigs and branches constantly appearing, older branches dying off, and with changes in the form of branches occurring frequently. Biologists regard plants and animals as two main branches of a family tree, the branches springing from a common, ancestral trunk.

When we attempt to define "plants" by separating them from animals, we find that our supposedly fixed definitive points assume the aspect of floating islands. None of us has difficulty in distinguishing between our pet dog and the roses in the garden. Yet, when we attempt to crystallize our instinctive knowledge into words, we tend to flounder. And if we slip down the scale of plant life, from the present day twigs, down the main branches and the trunk we find our task of definition becoming increasingly more difficult, until at last we reach a point at which we give up in despair, for the organisms which we encounter are neither plant nor animal, but possess characteristics of both. These creatures (one biologist has facetiously called them "plantimals") are probably very similar to some of the first organisms to appear on the earth.

If we disregard the lower "plantimal" organisms, what criteria, if any, may we use to separate the higher kinds of plants from the higher types of animals? Two, possibly three, criteria may be applied, all of them rather unsatisfactory ones, with numerous exceptions, but nevertheless the most useful which we can find.

In the first place, animals are unable to manufacture their own food. They are completely dependent upon plants, either directly (herbivorous animals) or indirectly (carnivorous animals), for their nutrition. In contrast, most plants are able to make their own food and are therefore more or less independent of external sources of food supply. There are, however, numerous plants — bacteria, molds, mushrooms, etc. — which are unable to make their own food and consequently, like animals, must obtain their food from external sources. We can say in general, however, that *most* plants possess the ability to synthesize complex organic substances from simple, inorganic materials, whereas animals lack this ability.

The basis of the food-synthesizing activity of most plants is the presence of chlorophyll, the green pigment which constitutes the mech-

anism by which carbohydrate foods are manufactured in the presence of sunlight. Animals lack this characteristic plant pigment. Plants which are able to manufacture food do so usually because they are equipped with chlorophyll. Not all plants possess chlorophyll or the ability to make food. Most bacteria, molds, mushrooms, and puffballs are plants which are unable to synthesize organic materials from inorganic. So we must make an exception in the statement of this difference between plants and animals and say that *most* plants possess chlorophyll, whereas animals do not, unless one admits that certain motile one-celled chlorophyllous organisms called **flagellates** are animals, as zoologists call them. Botanists call these flagellates plants because of their green color and their ability to make food, properties which are fundamentally plant characteristics.

A second difference sometimes proposed to distinguish between plants and animals is found in the method of growth. Animals possess a limited scheme of growth, in which the mature individual attains a certain maximum size and characteristic form, which undergo relatively little size change after maturity is achieved. In this limited type of growth, the living and non-living parts of the body maintain a fairly constant ratio, and virtually all embryonic, or growth, tissue is used up in the process of maturation, except certain small areas of such tissue available for regeneration. In plants, however, the maximum size attainable by members of a given species is exceedingly variable and depends in considerable degree upon conditions of the external environment. Further, the mature form, though it is rather characteristic of individual species, is similarly susceptible to the environment and exhibits wide variation. In the bodies of most plants embryonic tissues are abundant and active, and thus growth continues in many parts of the plant body, often over a period of many decades. The most active growth regions, those at the tips of roots and stems, are usually direct descendents of the embryonic tissues of the miniature plant in the seed. In this unlimited scheme of growth, the ratio of non-living tissue to living tissue constantly increases, in some plants over a period of many years, until the greater part of the body may be composed of dead tissues. As older tissues die, they usually remain in place and serve only for added strength and support; the young, active, growing tissues constantly grow away from the older, dead parts of the plant.

The third criterion which might be proposed to distinguish plants from animals is this: *most* plants (excepting some fungi and algae) are equipped with a structural framework of cellulose, a carbohydrate com-

pound which forms the major part of plant cell walls. Animals, with the exception of the Tunicates, degenerate descendants of the ancestors of the vertebrates, lack cellulose.

A fourth difference between most plants and most animals is the ability of the latter to move from place to place, as a result of their possession of nervous, muscular, and in the higher animals, skeletal systems. Higher plants are firmly anchored in the soil in which they grow, although in some primitive, microscopic plants, and in the sex-cells of some low and intermediate plant groups, locomotive ability is present. Similarly there are some exceptions in the animal kingdom, a number of primitive species of which pass their lives in a relatively immobile condition.

A study of these differences emphasizes the fact that there is no single difference which separates all plants from all animals. It is relatively easy to distinguish, on the basis of these differences, the higher types of plants from the more highly developed animals, but such distinction is difficult, often impossible, in the case of lower forms of organisms. The inevitable conclusion is that plants and animals are very similar in many ways and that they have arisen in their development from common ancestors.

SUMMARY

1. The characteristic properties of living things are:

    a. The power of assimilation — the incorporation of non-living substances into living matter.

    b. The quality of irritability — the sensitivity to external stimuli and the ability to react to those stimuli.

    c. The power of reproduction of similar kind.

    d. The ability to derive energy from substances called foods through the process of respiration.

    e. The cellular organization of plant and animal bodies.

2. Two principal theories have attempted to account for the nature of life:

    a. The Vitalistic Theory holds that living organisms possess a vital force which is qualitatively different from the forces active in non-living matter and that this vital force cannot be explained in terms of chemical and physical laws.

    b. The Mechanistic Theory holds that there is no mysterious vital force present in living organisms, but that all of the activities of organisms can be explained ultimately in terms of chemical and physical reactions.

3. The origin of life upon the earth has never been explained. Several theories have attempted to account for life's beginning:

a. The theory of spontaneous generation holds that living organisms can develop directly from non-living matter. This idea is not accepted by most biologists.

b. The theory which holds that life on earth came to this planet from some other planet.

c. The theory of Divine Creation, which holds that a Divine Being created living organisms from non-living matter.

4. The chief differences between plants and animals are:

a. Most plants are able to manufacture foods and other complex substances from raw materials of the air and soil, whereas animals lack this ability. Correlated with the ability of plants to make food is the presence of a green pigment, chlorophyll.

b. Plants have an unlimited scheme of growth, whereas animals generally have a limited scheme of growth.

c. Most plants have a structural framework composed chiefly of cellulose, a substance absent from the bodies of most animals.

d. Most plants are stationary, whereas most animals have the ability to move from place to place.

5. There is no single difference which separates all plants from all animals. Thus, it may be concluded that plants and animals are closely related and that they have probably had a common ancestry.

The Kinds of Plants

ONE OF the most conspicuous features of the plant world to the layman and botanist alike is the infinite variety of size, form, and behavior of its members. Plants vary in size from structurally simple, microscopic organisms, such as bacteria, some of which are only $\frac{1}{2}$ micron long by $\frac{1}{5}$ micron wide ($\frac{1}{50,000}$ of an inch by $\frac{1}{125,000}$ of an inch!) to seaweeds which may be several hundred feet long, and California redwoods, some of which attain heights of over 350 feet, diameters of thirty feet, and weights of twenty-one hundred tons. It is frequently reported that eucalyptus trees of Australia soar to heights of over 450 feet, but these reports have never been substantiated by reputable botanists. Thus the redwoods are the tallest known land plants. These bacteria and redwoods (with the closely related Big Tree (Figure 5)) of course possess the extremes of size in plants; all other species of plants are of magnitudes within these limits. In most cases, each species has a characteristic average size range, but plants are exceedingly susceptible to the molding influences of environmental conditions, and individuals are often larger or smaller than the average size of their species, depending upon the nature of the surroundings in which they have grown.

We customarily think of the seed-bearing plants as the largest of all plants. It is true that the largest known plants are seed plants, but there are some members of this group which are very small, much smaller in fact than many more primitive kinds of plants. The duckweeds (*Wolffia*) are seed plants, closely related to the Jack-in-the-Pulpit, which are found floating in ponds and aquaria in many parts of the world. Their dimensions are measurable in small fractions of an inch, yet they are green, make their own food, produce flowers, and form seeds, by means of which they are reproduced. Thus, the size of plants is no indicator of relationships or of evolutionary position.

The form of plants varies even more than does their size. There are known at the present time almost 340,000 distinct species of plants,
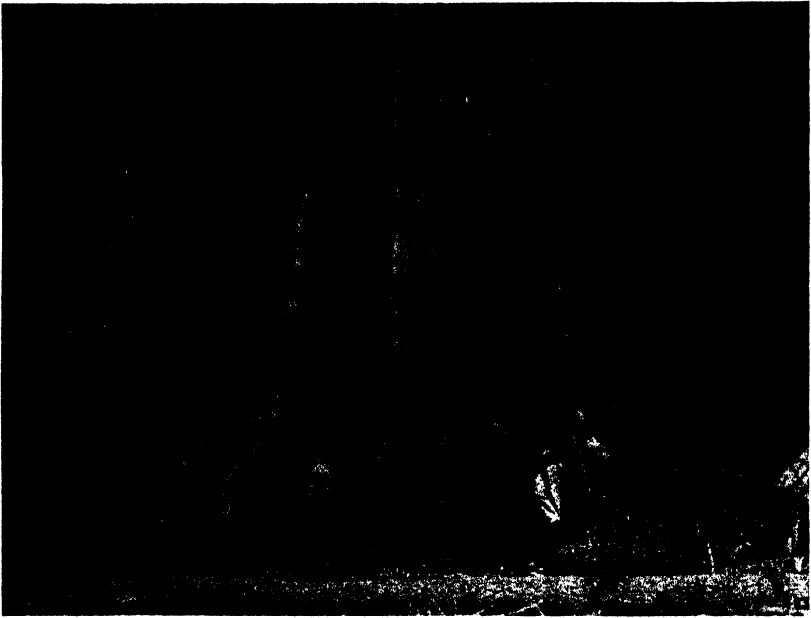
Photo by C. F. Hottes

Fig. 5. Base of trunk of California Big Tree.

many of these with numerous varieties differing very slightly from each other. Each species has its own characteristic habit of growth, shape of leaves, method of branching, form, and color of reproductive structures, and other peculiarities which give it a personality of its own and which enable us to distinguish it readily from other kinds of plants. Some plants are trees, others are woody vines, some are **herbaceous** (soft-stemmed) vines, still others are erect herbs. Some have large leaves, some small leaves, some, leaves with toothed or otherwise indented margins, some, leaves with smooth margins. Some have no leaves, but consist entirely of stems, roots, and flowers; others have simple bodies not differentiated into roots, stems, leaves, nor flowers.

Plants also differ among themselves in their behavior — that is, in the nature of their physiological processes, in their rates and methods of growth, and in their adjustment to their surroundings. The differences in size and form among plants are largely expressions of the fundamental physiological differences among various species, for the structure of organisms and physiological functions which they perform are inseparably related. Some plants grow very slowly; desert plants, for example, subjected to desiccating winds and scorching heat and

supplied with scanty quantities of water, grow so slowly that any increase in their size is noticeable only if they are examined at intervals of several years. In warm, moisture-soaked regions of the tropics, however, growth frequently proceeds at incredibly rapid rates. The leaf sheath of the banana plant grows for a time at the rate of $\frac{1}{25}$ of an inch per minute — that is, about $2\frac{1}{2}$ inches per hour. One of the most rapid rates of growth known in plants is found in the filaments of the **stamens** (pollen-bearing structures) of wheat flowers; these filaments, or stalks, for a brief time grow at about the same rate as the minute hand of a watch moves. These very slow and very rapid growth rates represent, of course, extremes. Most other plants grow more rapidly than stunted desert plants and more slowly than banana leaves or wheat stamens. There is also great variation in the rate of growth of different parts of a plant and also in the same parts at different stages in their development. Growth phenomena are highly sensitive to environmental factors and fluctuate greatly as external conditions change.

Plants also vary in other aspects of their physiology, particularly in the nature and relative quantities of their chemical products. All green plants manufacture sugar in the process of photosynthesis, but they utilize this sugar in different ways. Some convert the sugars to fatty substances which they store in their tissues; others transform sugars chiefly into starches as storage foods. Some plants elaborate large quantities of organic acids — for example, citric acid in lemons and oxalic acid in rhubarb. Some plants manufacture considerable amounts of aromatic oils — dill, for example, caraway, spearmint, sassafras, lavender, peppermint, and many other plants. Yellow pigments are manufactured in the petals of some flowers, red ones in others, blues and lavenders in still others, and, of course, the green pigment, chlorophyll, is generally present in leaves.

Another physiological difference among plants is found in their longevity. In some bacteria the existence of an individual endures only 20 or 30 minutes. At the end of this time, the bacterium reproduces and forms two new organisms, which in turn after the passage of a similar length of time, form offspring of their own. At the other extremes of age are certain coniferous trees, such as California Big Trees which attain ages of over 3,200 years. Many of our wild and cultivated plants are **annuals,** which live but a single growing season, some are **biennials,** which live through two seasons, and others are **perennials,** which continue to grow for many years. Trees and shrubs and many of our herbaceous plants, such as delphiniums and hardy chrysanthemums, are perennials.

One of the striking physiological differences among plants is found in their varying distribution in diverse habitats. Some plants live only in semi-arid deserts, others in the dripping rain-forests of the tropics. Some thrive on mountain tops, despite low temperatures and unrelenting winds, others flourish only at equatorial temperatures. There are some algae which grow most vigorously in hot springs, the temperature of which is not far below the boiling point of water. The sunflowers and most of their close relatives dwell in full, bright summer sunlight, while violets and wild geraniums grow best in shaded woodlands. Rhododendrons and azaleas are healthy only if the soil in which they are growing is acid, and greasewood, cliff fern, and beech make their best growth in soils which are more alkaline. Many plants, among them unfortunately a number of our most obnoxious weeds, are tolerant of great variation in the conditions of their environment and flourish under a wide range of external conditions. Others, like the rhododendrons and greasewood, are more sensitive and will react favorably only when the preferred conditions for growth are present.

Plants vary moreover in their methods of reproduction, and in the structure and development of their reproductive organs. These differences will be described in detail in subsequent chapters.

On the basis of their structural and reproductive differences, particularly the latter, plants are classified in groups intended to indicate something of their evolutionary positions and their mutual relationships (**phylogeny**). Reproductive differences are the principal criteria of systematic arrangement, for reproductive organs and processes are more stable and less liable to variation as environmental conditions change than are roots, stems, and leaves. Many plants may have superficially similar structure of roots, stems, and leaves, and yet they may differ strikingly from each other in their reproductive features. A study of books in **taxonomy,** or **systematic botany,** shows an important fact — namely, that plants are classified in different manners by different botanists. These differences in classificational schemes are attributable to differences in interpretation by botanists of the structures which they use as bases of classification. In attempts to erect a **natural** system of classification (one which groups plants according to their known or supposed natural relationships), difficulties frequently arise, because our knowledge of actual relationships is often meagre, due to the fact that there are many gaps in the evolutionary lines which natural systems attempt to follow. Consequently, even our most modern systems of classification are in part **artificial** — that is, when

actual relationships are not clear, their arrangements are based upon the convenience and expediency of the moment. Earlier attempts at classification were largely artificial. The more nearly natural systems have grown mainly within the last century, as the results of research have clarified many problems of relationships. Obviously, the ultimate goal of taxonomy is the replacement of artificial systems of classifications by natural systems.

The plant kingdom is customarily divided into 4 great groups, or divisions,[1] as follows:

1. THALLOPHYTA

These are the simplest of all plants from the structural standpoint. They lack roots, stems, and leaves. They are exceedingly variable in structure; some of them, the bacteria, for example, are very simple in form and are microscopic in size. Others, such as the sea-weeds, are very large and are rather complex morphologically. The thallophytes are further subdivided into the **algae** and **fungi.** The algae are principally water plants which contain chlorophyll and thus manufacture their own food. The fungi lack chlorophyll and hence must obtain their food from other living organisms (**parasitically**) or from the dead bodies or waste products of other organisms (**saprophytically**). Common members of the algae are pond-scums, sea-weeds, and the greenish organisms found on the bark of trees, on fence-posts, etc., usually on the shaded sides. The fungi include, in addition to bacteria, the yeasts, molds, mushrooms, rusts, smuts, and various other kinds of plants. There are approximately 30,000 known species of algae and 78,000 of fungi.

The Thallophyta really constitute an artificial group, for they are very heterogeneous in their structure, physiology, and reproductive methods. Recent investigations upon the structure, development, and physiological characteristics of the Thallophyta indicate that this division of the plant kingdom is composed of about 10 major subgroups (**phyla**). In an elementary course, the limitations of time and the lack of background on the part of students do not justify the detailed consideration of the complex relationships among these very diverse plants. Hence, for practical teaching purposes, the traditional, though phylogenetically faulty, treatment of the Thallophyta will be followed in this book. In the subsequent chapters on the thallophytes, the arti·

[1] See appendix for a modern classification of the plant kingdom.

ficial nature of this treatment will be demonstrated in discussions of the variations among these plants.

2. BRYOPHYTA

These are land plants, usually not more than a few inches in their greatest dimensions. They are green and hence manufacture their own food. They differ from Thallophyta in that their sex organs are larger and more complex structurally. They commonly possess small stem-like, leaf-like, and root-like structures, which are, however, much simpler morphologically than the roots, stems, and leaves of higher types of plants. Though the Bryophyta are chiefly land plants, they are limited principally to moist habitats. The bryophytes are separated into 2 groups, the **liverworts** and the **mosses,** of which there are about 8,800 and 14,000 species respectively.

3. PTERIDOPHYTA

These plants are chiefly land plants and considerably more complex in their structure than are the members of the two preceding divisions. There is a marked division of labor among the various parts of the plant body of the Pteridophyta. These parts are morphologically equivalent to the roots, stems, and leaves of the seed plants and are designated by these same names. The living pteridophytes, of which there are about 9,900 species, are subdivided into the **ferns, club-mosses,** and **horse-tails.** The ferns are the most numerous of the three groups. The pteridophytes, like the bryophytes, are able to complete their reproductive processes only in the presence of liquid water. There are no true seeds produced in the living pteridophytes, although a few pteridophytes develop structures resembling seeds of modern seed plants.

4. SPERMATOPHYTA

The outstanding characteristics of this group of plants are their reproduction by means of seeds and their extreme structural complexity and specialization. They constitute the dominant part of the present vegetation of the earth and are the plants of the greatest economic and historical significance to mankind. Their reproduction is independent of the presence of liquid water, a quality which enables them to grow

in many regions where many members of the other divisions are unable to survive. The exact number of species of seed plants is not known, for new species are constantly being described by botanists as new regions of the world are explored. There are probably 200,000 known species of spermatophytes at present. Thus, they constitute the largest of the four divisions of living plants. The spermatophytes are subdivided into the **angiosperms,** the seeds of which are enclosed by structures called **ovaries,** and the **gymnosperms,** in which the seeds are borne openly on the surfaces of scales, unenclosed by ovaries or similar structures. The gymnosperms number slightly more than 600 species and include the pines, firs, redwood, spruce, cedars, and their relatives. All the other species of seed plants are angiosperms, among which are our best known wild flowers, garden and crop plants, weeds, and broad-leaved trees. The characteristic reproductive structures of gymnosperms are called **cones,** those of angiosperms **flowers.**

SUMMARY

1. There are many kinds of plants on the earth.
2. These many types of plants vary principally in the following ways:
   a. Size.
   b. Form and structure.
   c. Behavior — physiological activities.
   d. Longevity. Annuals are plants which live through one growing season; biennials require two years to mature and then produce seeds and die; perennials live through a number of years.
   e. Distribution upon the surface of the earth.
   f. Methods of reproduction.
3. One of the goals of taxonomy is to determine the relationships among and ancestry of plants. The study of such relationships is termed phylogeny.
4. The plant kingdom is usually divided into 4 groups or divisions:
   a. Thallophyta: algae and fungi.
   b. Bryophyta: liverworts and mosses.
   c. Pteridophyta: ferns, horse-tails and club-mosses.
   d. Spermatophyta: gymnosperms and angiosperms.
5. The total number of known species of plants is over 335,000.

The Structure and Physiology of Flowering Plants

The Gross Structure and Activities of Seed Plants

SINCE THE seed plants constitute the most conspicuous and most familiar part of the earth's vegetation and since they are the plants of greatest importance in man's life, they will form the chief objects of our study in this book. We shall study their gross and minute structure and then reproductive methods, and their economic importance.

The bodies of most seed plants are composed of four kinds of structures: **roots, stems, leaves,** and **reproductive structures,** which are either cones or flowers. The roots, stems, and leaves are called **organs.** Cones and flowers should not be termed organs, since they are really specialized stems bearing structures comparable with leaves and concerned with reproductive processes; thus, cones and flowers are really clusters of organs. An organ may be defined as a major part of an organism, a part which performs a single main function or a group of closely related functions. Roots, stems, and leaves are termed the **vegetative organs** or a seed plant's body, because their functions center upon the intake of raw materials, the manufacture of food, and the utilization of food for growth and development. The vegetative organs have no direct role in the fundamental process of reproduction through the formation of seeds, although they may bring about the production of new plants by the growth and development of runners, underground stems, root "suckers," etc. Such multiplication of plants is termed **vegetative** reproduction. The parts of the cones and flowers concerned with the formation of seeds are the **reproductive organs.** In the angiosperms, flowers produce structures called **fruits,** within which the seeds are formed.

An intimate relationship exists between the vegetative and reproductive activities of plants. Every plant in its life-span, which extends from its inception as a seed to its death, passes through a series of physio-

logical stages. Vegetative activities — the absorption of raw materials, the manufacture of food, and the utilization of foods as sources of energy and building materials for growth — predominate during the greater portion of the life cycle in most plants. After these vegetative activities have proceeded for some time reproductive structures are formed and seeds are produced. One of the requisite conditions for the development of flowers or cones is a suitable food reserve, which is built up by vegetative processes. When reproductive functions begin, there is usually an accompanying decrease in vegetative activity, in part as a result of the movement of food reserves from vegetative organs into developing fruits and seeds. In **annual** plants (e.g., sweet peas, marigolds), a single season of a few weeks or months, most of the life-span is spent in vegetative activities; these are followed by the usually rapid formation of flowers and the production therefrom of fruits and seeds, which draw so heavily upon the food reserves of the vegetative parts of the plant that death of the plant usually results. The individual is sacrificed during the production of seeds, which maintain the species from generation to generation. In **biennial** plants (e.g., beets, carrots), a similar situation obtains, with this difference: the vegetative period extends through two growth seasons, during the second of which reproduction occurs, followed by the death of the plant. In **perennial** species (e.g., delphiniums, roses, apple trees), the individual has a life span of several to many years; during a brief period of one to several years immediately following the sprouting of the seed, activity is exclusively vegetative; when a food reserve has been built up, reproduction occurs. Thereafter during each year of its life the perennial plant carries on both vegetative and reproductive activities, ordinarily forming seeds during each year of its existence.

The gross and minute structure of these various organs varies greatly among the many species of seed plants. The major differences in the external and internal features of these organs will be discussed in subsequent chapters. It is sufficient at this point merely to consider briefly their general importance in the lives of typical seed plants.

The roots of most plants are non-green in color and usually grow beneath the surface of the soil. The principal functions of roots are the absorption of water and mineral salts from the soil, the anchorage of the plant body in the soil, and the conduction of materials upward into the stem and downward from the stem and leaves. In some plants, in addition to performing these functions, the roots store considerable quantities of food. There are other, more specialized functions of roots, which will be considered in detail in a later chapter.

Stems arise usually as branched continuations of the root system above the surface of the ground. Their structure varies greatly with different species of plants. The primary functions of stems are the conduction of materials upward, downward, and transversely, and the production and support of leaves and cones or flowers. In addition, most stems store food, and in some plants, if chlorophyll is present in the stem, these organs manufacture food. Other, more specialized functions of stems will be described later.

Leaves are outgrowths of stems and in their most common form are broad, flat, and thin, less frequently, needle-like or scale-like. The chief work of leaves is the manufacture of food by the processes of **photosynthesis,** though specialized types of leaves in some plants perform other functions. The term **shoot** is often applied to a stem with its leaves.

The bodies of seed plants, as described in the preceding chapter, are anchored in the soil or other material in which their roots grow. This immobility is attributed in part to the nature of the structural framework of plant bodies, which is composed largely of a rather tough, strong, elastic material called **cellulose.** The fixity of the positions in which plants grow places certain restrictions upon their activities and influences markedly their entire development and character, and, in some degree, their distribution upon the earth's surface. The limitations imposed by immobility influence significantly the operation of physiological processes in plants; plants can absorb water and various nutrients only from those portions of the soil penetrated by their roots. Exhaustion or diminution of these essential materials within the range of root systems results in the development of growth abnormalities which may lead to death. Fixity of position, moreover, limits the nature and extent of the responses which plants may make to changing environmental conditions. Thus, plants as individuals are less efficient than animals in making certain adjustments to surrounding conditions, particularly those involving the acquisition of nutrient substances.

SUMMARY

1. The bodies of seed plants consist of:
   a. Vegetative organs.
      Roots. Stems. Leaves.
   b. Reproductive structures.
      Flowers or cones. Flowers and cones are not organs but are groups of organs (stems and reproductive organs).

2. Vegetative organs are concerned primarily in the absorption of raw materials, the manufacture and utilization of foods, and growth. Reproductive structures (flowers and cones) produce seeds.

3. Reproduction of new plants is sometimes brought about by growth from vegetative organs and is called "vegetative reproduction."

4. In angiosperms, seeds are produced within structures called fruits.

5. In seed plants, vegetative activities precede the formation of seeds. Vegetative processes result in the accumulation of food stores which are necessary for the production of fruits and seeds.

6. Annual plants complete their life span in a single year or portion thereof. Biennial plants require two years for the completion of their lives. Annuals and biennials ordinarily flower and produce seeds only once. Perennial plants live for several to many years, producing flowers and seeds a number of times, commonly once a year.

7. The principal functions of roots are:
   a. Anchorage.
   b. Absorption of water and mineral salts from the soil.
   c. Conduction of substances.
   d. Food storage.

8. The principal functions of stems are:
   a. Conduction of substances.
   b. Production and support of leaves and flowers.
   c. Food storage.

9. The principal function of leaves is food manufacture. A stem with its leaves is termed a shoot.

10. The structural framework of plants consists of a system of cell walls, the principal constituent of which is an organic substance, cellulose.

The Microscopic Structure of Plants; Cells and Tissues

1. THE CELLULAR ORGANIZATION OF PLANTS

BOTANISTS HAVE been familiar for many centuries with the external forms of seed plants and the gross features of internal anatomy, but their knowledge of the details of the ultimate microscopic structure of plants is scarcely more than one hundred years old. The study of the microscopic features of plant bodies was made possible only after the invention and improvement of the magnifying lenses of microscopes. If one examines with the aid of a microscope a thin slice of tissue cut from a root or leaf or any other portion of a plant body, he observes immediately that the section is composed of very small compartments or **cells,** each of which consists of a **cell wall** surrounding a tiny droplet of living substance, or **protoplasm.** Similar microscopic study of thin portions of the bodies of all species of plants reveals fundamentally the same architectural plan — namely, the presence of cells as the basic units of structure in plants. All growth and development of an individual plant are the result of the formation of new cells from pre-existing cells. Further, in the production of offspring, certain cells become specialized in or on the body of a parent and subsequently separate from the parent plant. The newly formed offspring then begin a process of growth to maturity, a process which is the result of the formation and development of cells.

Even a cursory microscopic examination of plant sections shows that not all cells are alike, but that there is a considerable degree of variation in size and form among them. These size and structural differences are reflections of different functions which various cells perform. In the development of young, newly formed cells into mature cells there occurs a phenomenon termed **differentiation** or **maturation,** during which cells assume the different functions and structures which they

usually retain during the life of the organ of which they are parts. The processes taking place in cell differentiation involve a division of labor among cells; some cells become food-making cells, others function in the conduction of materials in plants, still others serve for strength, support, food storage, absorption, etc. The causes of this division of labor among cells are only incompletely understood; these causes seem to be due primarily to the hereditary characteristics of each species of plant and to the interaction between these hereditary traits and conditions of the external environment.

When botanists and zoologists first became aware that the bodies of plants and animals were composed of cells, they regarded these individual cells as of prime importance, the bodies which they constituted as aggregations of individual differentiated cells. They believed that the activities of the whole plant or animal might be considered as a summation of the activities of the individual, constituent cells. This idea, which was embodied in a statement known as the **Cell Theory,** might be compared with the Jeffersonian theory of democracy, which considered a nation as dependent upon and secondary in rights and privileges to the individual, component states. More recently, a biological interpretation, known as the **Organismal Theory,** has replaced in part the ideas expressed in the Cell Theory. Biologists who favor the Organismal Theory regard the entire organism, plant or animal, and not the individual cells, as the entity of prime importance and as the primary agent of organization. More specifically, they hold that a many-celled plant or animal is not merely a group of individualistic cells, but is rather an individual itself, a more or less continuous quantity of protoplasm, which, in the course of evolution, has become subdivided into cells. Cells are formed by differentiation within this mass of protoplasm; the individual is not the result of the aggregation of individual cells. Making use of the political analogy again, one might say that the Organismal Theory resembles that theory of government which holds the unified nation, not the states of which it is formed, to be of primary importance.

The Organismal Theory emphasizes a new biological concept which has developed partly as a result of physiological research upon correlation or the coordination of the various tissues and organs of living beings, upon the mutual interaction between different tissues and organs. In other words, these newer investigations have shown that the mere summation of the activities of individual cells does not explain sufficiently the behavior of organisms, but that there is a coordination

between cells which results in the entire organism's function as a unit. This coordination, this correlation of reactions arising above the separate activities of individual cells, is recognized by the Organismal Theory in its insistence upon the fundamental importance of the whole organism. This recognition is probably the principal reason for the increasing favor which the theory is finding.

In summary it appears that certain aspects of both theories may be accepted as an explanation of the basic morphological features of organisms. The Organismal Theory may be interpreted as a behavior doctrine. These ideas then may be incorporated into a unified biological theory which accounts for the ultimate microscopic structure of organisms, as well as for the correlated behavior of the structural units.

The bodies of seed plants are **multicellular** in nature; that is, there is a considerable degree of differentiation in structure and function among their component cells. Among certain of the Thallophyta there are organisms which consist of only a single cell (e.g., the bacteria). Such organisms are called **unicellular.** Frequently these unicellular organisms remain grouped together in aggregations termed **colonies.** Each of the cells in a colony is truly unicellular, because it carries on its own activities independently of neighboring cells. There is no division of labor and hence no structural differentiation among the cells of a colony. Such cells are usually able to continue their life activities if they become separated from all other cells of the colony.

2. THE SIZES OF CELLS

Plant cells are minute objects, most of them invisible to the naked eye, some of them so small that they appear merely as tiny spheres or rods under the highest magnifying power of the microscope. Most cells of higher plants vary between 0.1 and .01 of a millimeter ($\frac{1}{250}$ – $\frac{1}{2500}$ of an inch) in diameter. Between 4 and 40 such cells would just cover the period at the end of this sentence. Imagine the number of such cells in a tree. It has been calculated that a leaf of a full-grown apple tree contains 50,000,000 cells. Remember that such a tree possesses several thousands of leaves, a large trunk with numerous branches, flowers, fruit, and an extensive root system, and your mind will probably be unable to envisage the number of cells in the whole tree. Such a tree with a fairly large number of leaves — say 6,000 — would have 300,000,000,000 cells in the leaves alone. An apple fruit about 3 inches in diameter contains about 500,000,000 cells. If we assume a crop of

400 apples, then the total number of cells in the season's apple crop of one tree is 200,000,000,000. In the leaves and fruit alone, which constitute probably less than $\frac{1}{50}$th of the bulk of the whole tree, there are thus approximately 500,000,000,000 cells. If we accept the statement that the leaves and fruit constitute less than $\frac{1}{50}$th of the bulk of the tree (a conservative estimate), then a vigorous, full-grown apple tree would contain about 25,000,000,000,000 cells. The significance of this staggering figure becomes apparent if we realize that it is about 350 times the number of seconds since the birth of Christ! One botanist has estimated that it would require 90 years to take apart an apple leaf, removing cells at the rate of one cell per minute. When we think about the numbers of cells constituting the bodies of such huge trees as the western yellow pine and the California Big Tree, the figures become not merely appalling, but incomprehensible to us in their enormous size.

All cells, however, are not so small. In the stems of woody plants, fiber cells may often be found which are 6 to 8 millimeters in length. In the nettle family (*Urticaceae*), some cells may reach a length of 200 millimeters — about 8 inches. Such sizes, however, are rarities among plant cells. The great majority of them fall within the 0.1–.01 millimeter range.

3. THE STRUCTURE OF CELLS

Plant cells are extremely varied not only in size, but also with respect to their form, the functions which they perform, and the structures which they contain. If we examine with the microscope a green cell (Figure 6), such as that of a leaf, we find a number of structures which we may classify into three groups:

A. The **cell wall**, within which the living substance is contained.
B. The **protoplast**, or living substance of a single cell.
C. The **inclusions**, non-living materials present within the protoplasm.

A. THE CELL WALL

The cell wall is a comparatively strong and rigid structure arranged in the form of a box with at least six faces, or possessing a more or less spherical, ovoid, cylindrical, much elongated, or occasionally very irregular form. In spite of its great strength, the wall possesses a certain degree of elasticity which makes it possible for the wall to be stretched, compressed or twisted without its being broken. It is because cell walls

are so pliable and at the same time so strong, that stems and leaf stalks may be bent and buffeted by winds and yet return to their original form and position when the winds diminish. In multicellular plants, the cell walls form inter-connecting systems which are comparable functionally, and to a certain extent positionally, with the steel framework and walls of modern buildings. Plants lack the skeletal systems which are characteristic of higher types of animals, and their cell wall systems have the important function of giving strength and support to the plant body.

The cell wall is generally considered to be a non-living portion of the cell. It is composed of several kinds of chemical compounds which are manufactured and secreted by the protoplasm outside itself. The materials of which cell walls are composed are secreted in part by the protoplasm on one side of the wall, in part by the protoplasm on the other side. Thus, a cell wall may be compared with a wall in a house. The wall in a house is a double structure separating two rooms. When the wall is constructed some of the laths and plaster are applied from one room, and some are applied on the other side of the wall by a workman in the other room. In a similar manner the adjoining walls of two contiguous cells are secreted by the protoplasts of the two cells.

The first thin wall layer to be formed by young protoplasm is called the **middle lamella** or **intercellular layer.** This layer is composed chiefly of a group of chemical compounds called **pectic substances,** of which **calcium pectate** is the commonest. These pectic materials are exceedingly viscous and gelatinous in nature and they serve as a mucilage which holds the other wall layers, and thus the cells, together. Pectic materials are present in most fruits and are responsible for the "jelling" of fruit juices. Commercial preparations of pectic substances are often added to fruit juices in order to insure a uniform and satisfactory degree of hardening in the manufacture of jellies. As cells grow, other substances are deposited by the protoplasm in successive layers on the middle lamella. The individual layers which constitute the cell wall are so very thin that they are not distinguishable except under a microscope of unusual magnifying power and with special chemical treatment of the wall. Commonest of all solid substances in plant cell walls is **cellulose,** a **carbohydrate,** which is closely related chemically to starch and sugars. Cellulose will not dissolve in water, though it will absorb water in large quantities and allow it to pass freely into and out of the protoplasm. Cellulose is the substance mainly responsible for the tough, elastic nature of the cell wall. In addition to cellulose, these subse-

quently-formed layers of the cell wall may contain small quantities of minerals, **lignin, cutin, suberin,** and other materials. Lignin is an organic substance secreted into the walls of some cells, particularly those of wood. It is in a large part responsible for the hardness of wood. Cutin and suberin are waxy materials which are deposited extensively on and in the walls of cork and other types of cells; they render the cell wall in which they occur nearly impermeable to water. Cellulose constitutes as much as 75% of the dry weight of wood, and an even greater proportion of the fiber walls of cotton, hemp, and flax. Its economic value to man is thus very great, but its usefulness is not limited to its utilization in construction and in textile manufacture. Many other commercially important products of our present civilization are largely cellulose in nature; among these are paper, cellophane, celluloid, rayon, synthetic lacquers and varnishes, buttons, explosives, and others.
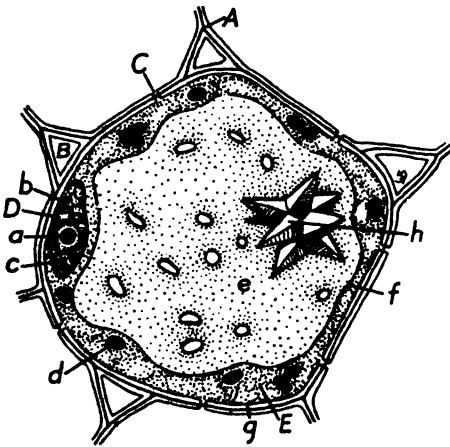

Fig. 6. Green plant cell

A. Cell wall. B. Intercellular space. C. Pit. D. Nucleus: a. nucleolus, b. chromatin network, c. nuclear membrane. E. Cytoplasm: d. chloroplast, e. vacuole, f. vacuolar membrane, g. plasma membrane, h. crystal.
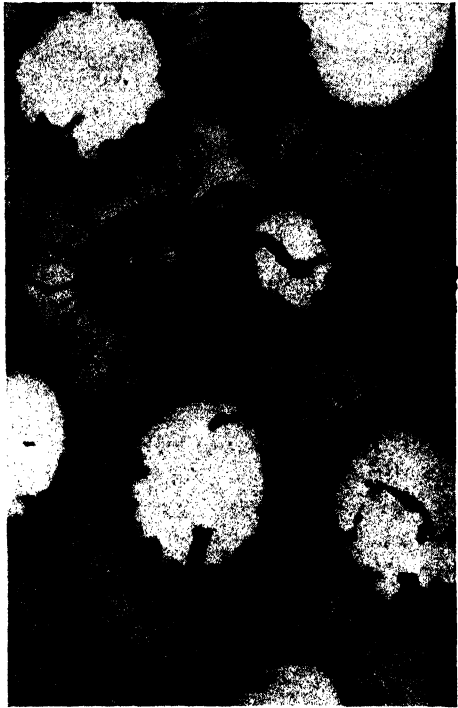
The thickness of cell walls varies greatly. In many cells, such as the green cells of leaves and the storage cells of roots, cell walls remain very thin, rarely more than a few thousandths of a millimeter in thickness. In other cells, such as the outer cells of date seeds, and the stone cells of peach stones, the walls become enormously thickened, so that at maturity the cavity within the cell wall is almost completely replaced by the thick cell wall.

The walls of most cells are not uniformly continuous. In many kinds of cells, especially in wood, the secondary wall layers do not develop at certain points. Thus, minute thin areas are left in the cell wall. These thin areas are called **pits** and they facilitate the passage of water and dissolved materials from cell to cell. In many types of cells exceedingly small canals pass through the wall layers and through these pores delicate strands of protoplasm called **plasmodesmata** (Figure 7) extend

from the protoplasm of one cell to that of another. These protoplasmic connections are important in the interchange of foods and other materials between cells and also in the transmission of excitations initiated by environmental stimuli. Plasmodesmata are so very fine and delicate that they usually cannot be seen with ordinary student microscopes. Their presence is exceedingly difficult to demonstrate and for this reason our knowledge as to the extent of their occurrence in plant cells is fragmentary. It is probable that they are much more common than their demonstrated presence seems to indicate.

Fig. 7. Plasmodesmata extending through thickened cell walls of persimmon endosperm (food-storage tissue of seed).

In the structure of the cell wall of plants, we find one of the striking differences between most plants and animals. The rigid, cellulose walls of plant cells have no counterpart in animal cells, which have no walls, but only a fragile living membrane surrounding the protoplasm.

B. THE PROTOPLAST

All the physiological processes of living organisms occur in the living substance, protoplasm, that material which the famous English biologist, Huxley, called the "physical basis of life." Protoplasm is a liquid of viscosity varying from that of fresh white-of-egg or thin syrup to that of semi-solidified gelatin. It is elastic, somewhat mucilaginous in texture, and usually transparent and colorless. The elasticity and viscosity vary with changes in internal conditions (age, condition of health, rate of physiological activity, amount of food stored, etc.) and external conditions (temperature, chemical agents, light, etc.).

Careful examination of the living protoplasm of a typical plant cell, such as a leaf cell, shows that the **protoplast** is not homogeneous, but that it contains a variety of visible structures within it. Some of these are non-living materials (**inclusions**), others are differentiated living parts of the protoplasm. Most conspicuous of these living structures is the **nucleus,** which appears as a rather large spherical, ovoid, or sometimes elongated structure in the protoplasm. In most kinds of organisms there is one nucleus in each cell. In some bacteria and algae, no nuclei are present, but some of the characteristic chemical substances present in nuclei are found scattered through the protoplasm of such cells. In a few types of plants, some of the algae and lower groups of fungi, for example, there may be several or many nuclei in each cell. The nucleus is colorless, transparent and generally more viscous than the remainder of the protoplasm. It may move about within the protoplasm and frequently changes its shape as it does so. The living nuclear contents appear homogeneous, but if they are stained with dyes which color the nucleus, it becomes apparent that the nucleus, like the whole protoplast, is not structurally uniform but is made up of several distinct parts. A very thin, tenuous **nuclear membrane** delimits the nuclear contents from other portions of the protoplasm. The liquid material within the nucleus is called the **nuclear sap.** Enclosed by the nuclear membrane and bathed in the nuclear sap is visible a small, spherical **nucleolus** (some nuclei contain more than one nucleolus), the function of which is not known with certainty. Some experimental evidence indicates that the nucleolus is probably a concentrated bit of stored food, which can be utilized by the protoplasm in case of starvation. Also within the nuclear membrane is present a granular substance called **chromatin,** which is usually present in the form of a diffuse, irregular network that becomes apparent only after the addition of suitable stains to the cell. The chromatin is the principal substance of the cell involved in the control and transmission of most hereditary characteristics from cell to cell and from parent organism to offspring.

The nucleus apparently functions as a directive and controlling center of the major physiological activities of the cell. Cells from which the nuclei have been removed by micro-dissection soon exhibit physiological abnormalities, resulting after a time in the death of the cells. Among the chief activities controlled by the nucleus is the regulation and transmission of hereditary characteristics, a function which will be described in detail in the next chapter in connection with the process of formation of new nuclei.

All the remaining protoplasm outside the nucleus and in which the nucleus is embedded is called **cytoplasm.** The term cytoplasm is one of convenience, used to refer to the greater bulk of the protoplasm, that outside the nucleus. It is in the cytoplasm that many of the chemical and physical changes involved in the physiological processes of cells occur. In very young cells, the cytoplasm occupies most of the volume of the cell, except, of course, the space occupied by the nucleus. As cells become older and grow markedly in size, the cytoplasm fails to increase in quantity proportionately and forms a thin layer in the outer part of the cell cavity, lining the cell wall. The central region of the cell, that inside the cytoplasmic layer, becomes a **vacuole,** a clear structure, which is filled by a watery solution, the **cell sap.** These terms are used as synonyms by some botanists, but more frequently, the word **vacuole** is reserved for the cavity, **cell sap** for the liquid which fills it. The vacuole and cell sap are non-living parts of the cell and hence are inclusions, not parts of the living cytoplasm. The cytoplasm, being a part of the proto-plasm, exhibits the same properties described earlier in this chapter — a mucilaginous texture, elasticity, transparency, etc.

The surface of the cytoplasm, the portion just inside of the cell wall, and likewise the portions of the cytoplasm bordering upon the vacuoles are often somewhat clearer than the other parts of the cytoplasm. These clearer parts of the cytoplasm are not readily demonstrated, but because of certain aspects of the physiological behavior of cytoplasm, the presence of such distinct surface layers between the cytoplasm and the cell wall and between the cytoplasm and the vacuole is usually assumed. These thin layers are called **cytoplasmic membranes** and they are exceedingly important in cellular physiology in that they control in a large degree the passage of materials into and out of the living protoplasm. In order to distinguish positionally between the cytoplasmic membranes, the membrane on the surface of the cytoplasm is usually called the **plasma membrane,** that separating cytoplasm from vacuole, the **vacuolar membrane.**

Also of importance among the living structures of the cytoplasm are the **plastids,** definitely organized bodies which are usually spherical or ovoid in form, less frequently ribbon-like or collar-shaped. Most plastids are clearly visible in the living condition; no dyes are required to make them visible, as is the case with the parts of the nucleus. The plastids which vary in number from one to dozens per cell, are of three types: **chromoplast(id)s, leucoplast(id)s,** and **chloroplast(id)s.** Chromo-plasts are red, yellow, or orange in color, and appear most commonly

in the petals of many kinds of flowers, in fruits, such as the tomato and red pepper, and in other plant parts. The characteristic colors of chromoplasts are attributable chiefly to the presence of two pigments, **carotin** and **xanthophyll,** respectively deep and pale yellow in color. The exact functional significance of these pigments and chromoplasts is not understood, but there is experimental evidence that carotin is converted into vitamin A in animals. Plants such as carrots, lettuce and spinach, which promote the formation of vitamin A in animals, are rich in carotin. The role played by these pigments in plant cells is not known. It is thought that they may have some significance in food manufacture or in sexual reproduction, but evidence for positive conclusions is lacking. Leucoplasts are colorless plastids, occurring most commonly in storage cells of roots and underground stems. They are centers of starch grain formation in these storage cells. Chloroplasts are the most common of the three kinds of plastids, occurring in virtually all green cells, except in one group of algae. The green color of chloroplasts is caused by the green pigment, **chlorophyll,** which is really a mixture of two slightly different pigments, **chlorophyll A** and **chlorophyll B.** Carotin and xanthophyll are also present in chloroplasts, but their color is masked by that of the more abundant chlorophyll. Chloroplasts by virtue of the chlorophyll which they contain, are the mechanisms of carbohydrate-food manufacture in plants.

It is interesting physiologically that plastids of one kind under certain conditions are transformed into other types of plastids. In tomatoes, for example, leucoplasts are present in the tiny, undeveloped fruits. As the fruits enlarge, the leucoplasts slowly develop into chloroplasts, and in the last phases of ripening the chloroplasts are changed into chromoplasts, which are responsible for the color of the fully ripened fruits.

In addition to plastids, smaller, rod-shaped or granular structures, called **chondriosomes,** or **mitochondria,** are generally present in plant cells. These structures are invisible in living cells and appear only when the cells are stained with certain dyes. The function of chondriosomes is not known, although in some cases, plastids seem to develop from them.

C. INCLUSIONS

These non-living bodies in cells are not actually part of the living protoplasm, but they may be necessary for its normal physiological activities. Some of them may thus be compared with the oil and gaso-

line necessary for the proper functioning of an automobile. The lubricant and fuel are not actually a part of the automobile's mechanism, but they are necessary for its operation. Among the most frequent kinds of inclusions in plant cells are vacuoles and the cell sap which they contain, crystals, and stored foods in solid form, such as starch grains, protein bodies, and oil drops. Crystals are found usually within vacuoles, rather than in cytoplasm. Crystals and certain other types of inclusions are apparently waste materials of physiological activity of the protoplasm.

4. TISSUES

As has been emphasized in a preceding section, the cells of plants show great variations in size and structure, differences which reflect the diverse functions of these cells in the physiology of the plant. A group of cells performing essentially the same function and commonly of similar structure, is called a **tissue**. An organ, such as a leaf or root, is composed of **tissues**; usually in an organ the various tissues perform interrelated functions. Tissues are classified on different bases — on their origin, their structure, or their physiology. A satisfactory classification, based on morphological and physiological features, is the following:

    1. EMBRYONIC (MERISTEMATIC) TISSUES.
    2. PERMANENT TISSUES
        A. SIMPLE PERMANENT TISSUES (Figure 8)
            a. EPIDERMIS
            b. PARENCHYMA
            c. SCLERENCHYMA
            d. COLLENCHYMA
            e. CORK
        B. COMPLEX PERMANENT TISSUES
            a. XYLEM (Figures 9, 10)
            b. PHLOEM (Figure 11)

Embryonic (meristematic) tissues are located near the tips of roots and in the buds at tips of stems, between the bark and wood of trees, in the bark of trees, and elsewhere in the bodies of plants, wherever extensive growth occurs. The embryonic tissues at the tips of roots and of stems are called the **growing points**, or **terminal meristems**; these cause growth in stems and roots. The embryonic tissue between the wood and the bark is called the **cambium**, which causes growth in diameter of stems, and the embryonic tissue in the bark is called the
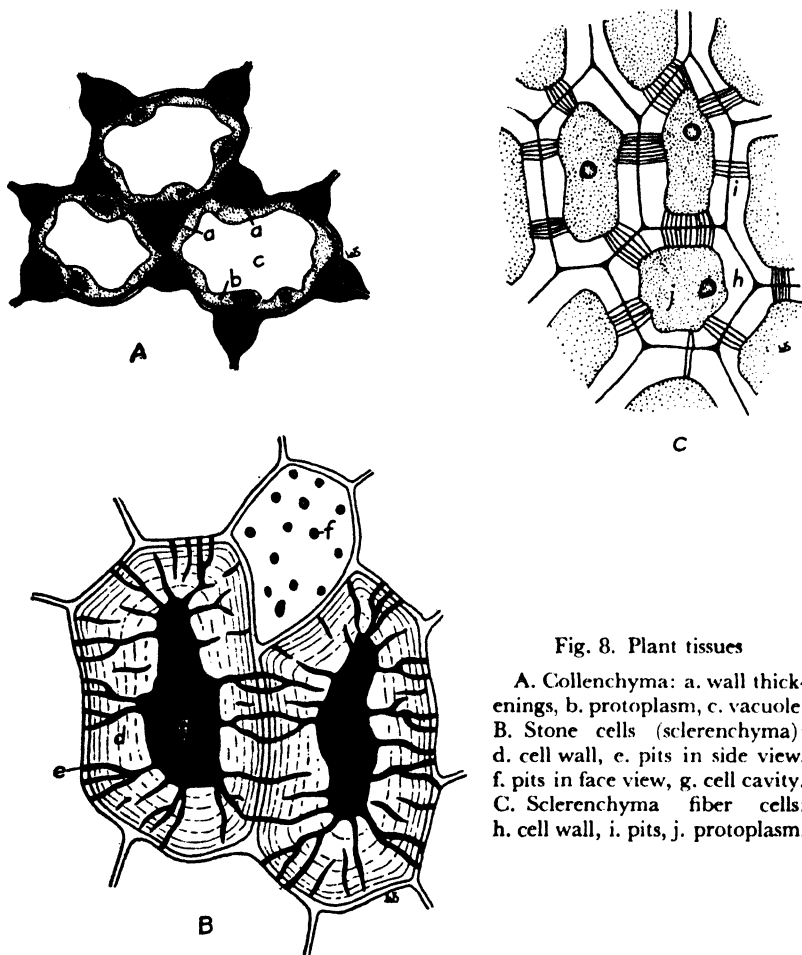
Fig. 8. Plant tissues

A. Collenchyma: a. wall thick-
enings, b. protoplasm, c. vacuole.
B. Stone cells (sclerenchyma):
d. cell wall, e. pits in side view,
f. pits in face view, g. cell cavity.
C. Sclerenchyma fiber cells:
h. cell wall, i. pits, j. protoplasm.

cork cambium. This last-named tissue produces the outer bark of trees
and shrubs. These embryonic tissues are composed of actively growing
cells which form new cells by a process known as **cell division.** Em-
bryonic cells are small, thin-walled, commonly cubical or nearly so in
form, although cambial cells are very much elongated, and contain
very dense protoplasm, the vacuoles of which are small and often in-
visible. These cells are tightly packed and usually without intercellular
spaces. Newly-formed cells, by processes of enlargement and morpho-
logical differentiation, become transformed into the mature, permanent
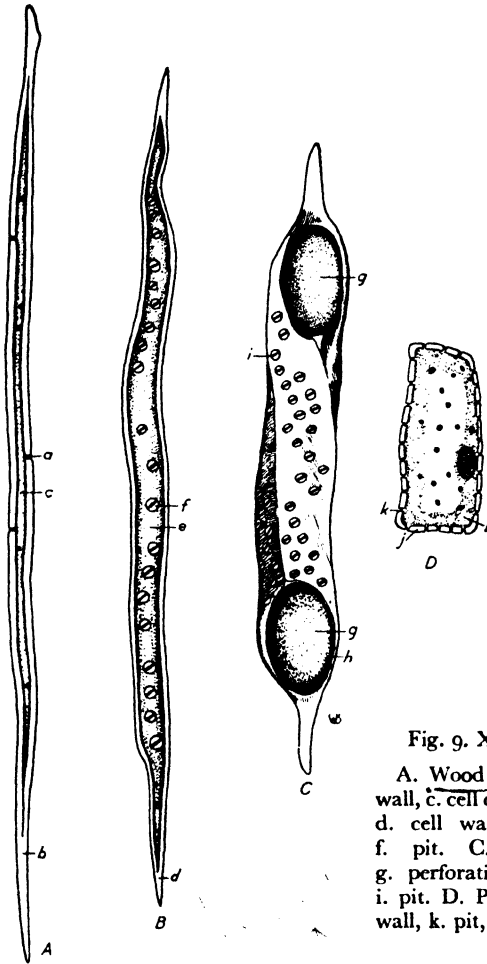tissues of plants.

Fig. 9. Xylem cell types

A. Wood fiber: a. pit, b. cell wall, c. cell cavity. B. Tracheid: d. cell wall, e. cell cavity, f. pit. C. Vessel element: g. perforations, h. cell wall, i. pit. D. Parenchyma: j. cell wall, k. pit, l. protoplasm.

Permanent tissues are so-called because they do not usually become changed into other kinds of tissues, as do meristematic tissues, but in most cases retain their structural and physiological characteristics for the entire life of the organ of which they are parts. Simple permanent tissues are those in which all of the constituent cells are similar structurally. The **epidermis** is a kind of permanent tissue which is usually only one cell thick and which forms the surface layer of leaves, flower parts, and the younger parts of stems and roots which do not have bark. The epidermis of the aerial parts of plants functions primarily in conserving the moisture supply of the inner tissues and in offering
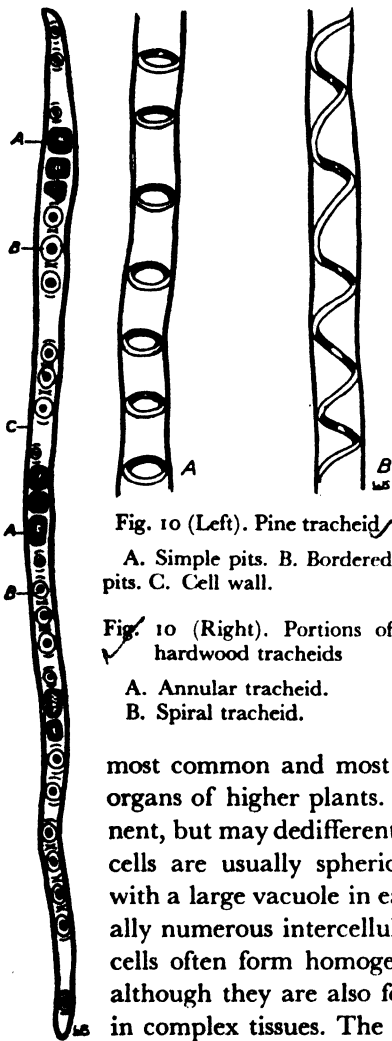
Fig. 10 (Left). Pine tracheid

A. Simple pits. B. Bordered pits. C. Cell wall.

Fig. 10 (Right). Portions of hardwood tracheids

A. Annular tracheid.
B. Spiral tracheid.

a certain amount of protection against mechanical injury and the entrance of parasites. The outer walls of these cells are often rather thick and are in most cases covered by a layer of cutin, a waxy, waterproof substance secreted by the protoplasm of the epidermal cells. Epidermal cells, except the **guard cells,** which control the epidermal pores or **stomata,** are generally colorless. Occasionally bluish, red or purple pigments may be present in the cell sap of epidermal cells and may thus give the leaves in which they occur a like color, as in purple-leafed cabbage and the variegated leaves of *Coleus.* The guard cells contain chloroplasts and are thus the only green cells of the epidermis.

Of the simple, permanent tissues, parenchyma tissue is the most common and most abundant, occurring in virtually all organs of higher plants. Parenchyma tissue is usually permanent, but may dedifferentiate and become meristematic. These cells are usually spherical, ovoid or sometimes cylindrical, with a large vacuole in each cell, very thin cell walls, and usually numerous intercellular spaces among them. Parenchyma cells often form homogeneous tissues of considerable extent, although they are also found mixed with other types of cells in complex tissues. The parenchyma cells of roots and stems, such as those of pith, are usually colorless and function chiefly in the storage of foods and water. Parenchyma cells form the greater part of the internal tissues of leaves, in which case they contain chloroplasts and manufacture food. Parenchyma cells retain their living protoplasm for a long time; in some species of cacti, cells of this type achieve ages of over a century.

Sclerenchyma tissue is also tissue of the simple, permanent type. There are two types of cells found in such tissues, **fibers** and **stone cells,**

the function of which is the provision of strength and mechanical support. Both kinds of cells have greatly thickened walls, the cellulose and lignin of which are secreted by the protoplasts of these cells. The protoplasts die when the walls reach their maximum thickness. Fibers are much elongated cells, with tapering ends. They possess great strength and flexibility. Because of the cohesive powers of adjacent fibers and their strength and pliability, these cells are used by man in the manufacture of twine, rope, mats, and various types of textiles. The fibers of linen and the hemps are sclerenchyma cells of the stems of these plants. Stone cells resemble fibers in that their walls are very thick and tough, but they are not elongated as are fiber cells. Stone cells form the major part of walnut shells and those of other kinds of nuts, they form gritty masses in the skin and pulp of pears, and they constitute an important part of the bark of trees.

Another simple, permanent tissue is **collenchyma,** made up of cells which remain alive for long periods of time and which have walls thickened at the corners. Collenchyma is the earliest strengthening tissue to become differentiated and thus occurs in the younger parts of plants, as well as in older parts. Cells of this type are frequently elongated, but not so markedly as are fibers.

Cork tissue is likewise a simple, permanent tissue. It forms the outer bark of the stems and roots of woody plants, and is a protective tissue which guards against mechanical injury of the inner bark and cambium, and against excessive evaporation from the inner living tissues. The protoplasm of cork cells dies very early after the cells are formed by the cork cambium; thus, mature cork cells are dead. Before the protoplasm dies, it secretes a waterproof substance, **suberin,** into the cell wall; this is responsible for the waterproof nature of these cells.

Complex tissues are those in which several kinds of cells occur, in contrast to simple tissues, which are made up of a single type of cell. In complex tissues, the various kinds of cells usually engage in a group of closely related activities. The complex tissues of plants are called **xylem** and **phloem,** both of which function as conducting and strengthening tissues. Xylem conducts water, dissolved mineral salts, and, at certain times, foods upward through stems; phloem carries mainly foods, which have been manufactured in the leaves, downward into the lower portions of the stems and roots. There is experimental evidence that in some plants a certain amount of the upward conduction of mineral salts and foods is by way of the phloem. Xylem is composed of **tracheids, vessels, ray cells, fibers, and xylem parenchyma,** the latter two
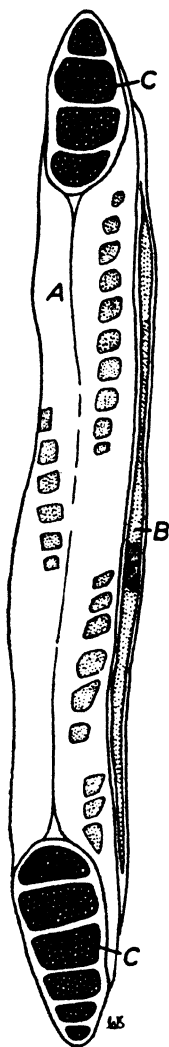
of which were described earlier. Tracheids are elongated, tapering cells, the protoplasm of which dies shortly after the cells are formed. The walls of many tracheids are thickened by spirals or rings of lignocellulose, and often possess thin areas or pits. In certain kinds of plants, the gymnosperms, for example, the xylem is made up almost entirely of tracheids which thus form the chief conducting portion of the tissue. Vessels are not single cells but are long, vertical tubes, sometimes a yard or more in length, composed of elongated cylindrical vessel cells which are arranged end to end and from which the end walls have been digested. Vessels often have pits in their walls and frequently contain various forms of thickenings, as do tracheids. The thickened areas in the walls of vessels and tracheids give added strength to the xylem tissue. Vessels are the principal conducting structures in the xylem of most angiosperms. Ray cells are chiefly parenchymatous.

The phloem always contains two types of cells, **sieve tubes** and **phloem parenchyma** and commonly, in addition, **companion cells** and **fibers.** Sieve tubes, like xylem vessels, are vertically elongated rows of cylindrical cells, the end-walls of which contain numerous, usually circular perforations like those in a sieve. These sieve tubes contain living protoplasm, from which the nuclei are absent at maturity. The cytoplasm is continuous from cell to cell through the sieve pores of the end walls. Sieve tubes are the principal conducting cells of the phloem. In most seed plants, companion cells, which are likewise vertically elongated, but usually somewhat shorter and smaller in diameter than sieve tubes, are found bordering upon the latter. Like the sieve tubes, they are living, but they retain their nuclei throughout their lives. Since there are perforations in the walls between sieve tubes and companion cells, it is believed that the latter may aid the sieve tubes in conduction or may store foods. Phloem parenchyma and ray cells likewise store food, and phloem fibers are strengthening and supporting cells.

Fig. 11. Sieve tube cell with companion cell

A. Sieve tube cell.
B. Companion cell.
C. Sieve plates.

A study of the structure of these various tissues illustrates strikingly the inseparable connection between form and function. Cells which furnish strength and support are thick walled, elongated, tough, and flexible. Conducting cells have in their walls thin areas and perforations which facilitate the transportation of materials from cell to cell. Protective cells, such as cork, are dead at maturity, are frequently formed in considerable thicknesses, and are waterproofed so that they reduce or eliminate evaporation of moisture from the underlying tissues. The study of morphology alone, without consideration of physiological activities is as meaningless as the study of functional processes without references to the structure of the cells and tissues which perform them.

SUMMARY

1. The bodies of plants are composed of structural units called cells.

2. A living cell consists of a cell-wall, composed largely of cellulose, and a living substance, protoplasm, within the cell wall.

3. All growth and reproduction of plants involves the formation of new cells from pre-existing cells.

4. Cells differ greatly in their structure and functions; these differences develop as a result of processes of differentiation or maturation.

5. The Cell Theory regards a plant or animal as an aggregation of cells. The Organismal Theory regards the whole organism as a unit, which is subdivided into functional units, or cells.

6. Some plants consist of one cell; these are called unicellular plants. Frequently unicellular plants remain grouped together in colonies; there is no division of labor among the cells of a colony. A multicellular plant consists of many cells, among which structural and physiological differentiation occur.

7. Most plant cells vary in diameter from $\frac{1}{250} - \frac{1}{2500}$ of an inch. Fiber cells sometimes attain lengths of several inches.

8. Cell walls are considered non-living secretions of the protoplasm within. They consist of several layers of substances — a central (intercellular) layer, composed chiefly of pectic substances, and secondary layers, consisting chiefly of cellulose.

9. Cell walls are tough and strong, yet somewhat elastic, and give strength and support to plant bodies.

10. Cell walls frequently contain thin areas (pits) and canals which extend completely through them. Strands of protoplasm (plasmodesmata) commonly extend through these canals from cell to cell.

11. Living protoplasm is a slimy, somewhat viscous liquid, containing various microscopically-visible structures, some living, others non-living (inclusions).

12. Most conspicuous of the living structures in protoplasm is the nucleus, a directive center of most cellular activities. A nucleus is separated from the remainder of the protoplasm (cytoplasm) by a nuclear membrane, and contains nuclear sap and chromatin, a substance intimately involved in inheritance, one or more nucleoli.

13. All of the protoplasm outside the nucleus is cytoplasm. This contains a number of structures, among which are:

    a. Plastids — chromo-, chloro-, and leuco-.

    b. Cytoplasmic membranes — on the surface of the cytoplasm and between cytoplasm and vacuoles.

    c. Inclusions — starch grains, crystals, vacuoles (small droplets of dissolved materials), oil droplets, etc.

14. Chloroplasts contain the green pigment, chlorophyll, and are centers of sugar manufacture (photosynthesis).

15. Chromoplasts are orange-reddish structures, the exact significance of which is not known. Leucoplasts are colorless and are centers of starch storage.

16. A group of cells with usually similar structure and closely related functions is called a tissue. The principal plant tissues are:

    A. Embryonic (meristematic tissues).

    B. Permanent tissues.

        a. Simple permanent tissues.
        Epidermis, parenchyma, sclerenchyma, collenchyma, cork.

        b. Complex permanent tissues.
        Xylem, phloem.

The Physiology of Plant Cells

1. PHYSICO-CHEMICAL NATURE OF PROTOPLASM

IT WAS mentioned in the preceding chapter that protoplasm is a rather viscous, transparent, colorless liquid, the consistency of which varies from time to time. Protoplasm from the physical standpoint is not a true solution, but is a **colloidal** system. In a colloidal system, the particles present are not individual molecules, separated from each other, as in a sugar solution, but are aggregations of molecules; these aggregations are sometimes large enough to be detected under a microscope, but are usually too small to be seen even under high-power magnifying lenses. In such cases, the presence of particles of supra-molecular size is inferred by the turbidity which such particles give to their liquids in which they are present, or by the reflection of light rays from their surfaces, or by other aspects of their physical behavior. Colloidal particles may be suspended in gases, in solids, or in liquids, most frequently the latter. These particles in some cases may remain suspended indefinitely in the medium in which they are present, without any settling-out. In other colloidal systems, the particles are exceedingly unstable and may be caused to precipitate by slight changes in the chemical or physical nature of the medium. Colloidal systems may be in liquid condition, as in the protein-in-water colloidal system of egg-white, or they may be semi-solid, as in gelatin desserts. The former colloidal state is termed a **sol,** the latter a **gel.** Protoplasm is for the most part a sol, though under certain conditions it loses its liquid quality and becomes a gel. Such changes in the colloidal state of protoplasm are often reversible and are induced in large part by changes in external factors, such as temperature, acidity, certain types of light rays, etc., and in part by internal changes. Sometimes the gelation of a colloidal sol is not reversible, as, for example, when egg-white is coagulated by boiling

water. Coagulation is thus an irreversible colloidal gelation and results in the death of protoplasm.

The greater part of living protoplasm exists in a colloidal condition, although there is some material present in true solution. Because of the infinite complexity of colloidal systems, because of the great surface attraction of certain colloidal particles for various molecules and ions, because of the development of electric charges upon colloidal particles, because of the frequent instability of such particles, many varied chemical and physical reactions can proceed simultaneously in different parts of the same protoplast. These colloidal systems of the protoplasm and cell walls are capable of absorbing large quantities of water and of holding them tenaciously against drying forces, just as a gelatin preparation, or a mass of cherry gum from the surface of a cherry trunk, remains moist for several days after being removed from a supply of water and exposed to dry air. In living protoplasm the liquid in which the colloidal particles are dispersed is of course water; the particles themselves are principally proteinaceous and fatty in nature.

The most careful chemical analyses of living protoplasm have never presented a completely accurate account of all of the kinds of chemical compounds present in protoplasm and the exact proportion in which they occur, for protoplasm is so unstable and so sensitive to external conditions that the first stages in the analytical processes applied to it doubtless bring about sudden alterations in many of its constituents. Thus, chemical analyses of protoplasm must be interpreted as analyses of *dead* protoplasm, killed by the analytical process and therefore different from protoplasm in the living condition. Such analyses, however, do indicate the kinds of chemical *elements* present in living protoplasm, the relative proportions in which they occur, and also the nature and amounts present of the more stable chemical compounds.

Certain chemical elements are present in all living protoplasm, both plant and animal. Most abundant of these are oxygen, carbon, hydrogen, and nitrogen, listed in the descending order of their abundance. These four elements ordinarily constitute 95–98% of active, living protoplasm. In addition, other chemical elements, probably always present (in green plants, at least), in smaller quantities, are sulphur, phosphorus, calcium, magnesium, potassium, and iron. Still other elements commonly, possibly always, present in plant protoplasm are chlorine, zinc, aluminum, copper, boron, and manganese, these latter present in very minute quantities. All of the elements thus far listed are physiologically significant, and perform definite functions, at least in

green plants. Frequently chemical analyses show the presence in plant tissues, of other elements such as nickel, gold, tin, mercury and others. These elements are apparently of no importance in the physiology of plants, in fact, they may even be toxic to the plants which have absorbed them from the soil. Such elements are found in plants because they happened to be present in the soil in which the plants grew and because the plants were unable to prevent their absorption. Thus, the mere presence of certain chemical elements does not imply that all such elements are useful in the plant's economy.

At a recent meeting (1939) of geologists in Canada, one mining geologist reported that he had made use of plants as indicators of the location of gold and other precious metals in soils. Since plants absorb such substances, at least in small quantities if they occur in the soil, the presence of these elements in plant tissues as indicated by chemical analyses is evidence that the soil in which the plants grow contains these substances. According to the results presented by this geologist, chemical analyses of plant tissue have been used successfully in locating deposits of gold, silver, tungsten, molybdenum, vanadium, nickel, tin, and several other valuable minerals. Whether or not this method of prospecting for minerals will prove commercially successful, it is an interesting variation upon the oft-quoted theme of "sermons in stones and tongues in trees."

These chemical elements for the most part do not occur in elemental form in protoplasm but are combined in the form of chemical compounds. Water is the most abundant chemical compound in active protoplasm, varying in percentage from 70 to 95. In dormant tissues, such as those of seeds, however, the water content may be as low as 4 or 5%. Of the solid material in protoplasm, **proteins** constitute the greater part. These fundamental components of protoplasm are foods which are rich in nitrogen and which frequently contain also, in addition to the carbon, hydrogen, and oxygen in their molecules, phosphorus and sulphur. Proteins are very complex and diverse chemically, and information concerning the details of the chemistry of protein compounds present in protoplasm is scanty. In addition to proteins, many other kinds of chemical compounds are present in living cells. Common among these are sugars, starch, fats, organic acids, mineral salts, pigments, alkaloids, and numerous others. Some of these, particularly certain fatty substances, are important fundamental protoplasmic constituents, together with the proteins as mentioned above. Most of these substances, however, are not actually constituents of living proto-

plasm; some of them, such as alkaloids and certain organic acids, are apparently by-products of physiological processes, others are raw materials which the protoplasm builds up into foods, still others are foods used as sources of energy or assimilated into living protoplasm. Such compounds are the fuel, lubricants, and exhaust of the proto-plasmic machine.

A notable fact concerning the chemical constitution of living protoplasm is the impossibility of classifying the individual constituent compounds as living or non-living. Every single chemical compound, isolated from all others in protoplasm, is non-living. Only when certain of these, chiefly the proteins and certain fatty materials, are present together in the proper organization does the living condition exist. The intricacies of this organization are unknown to us, for in the process of laboratory analysis, the organization itself is destroyed. Thus, any effort to separate protoplasmic chemical compounds into living and non-living is both unfeasible and meaningless.

2. THE ABSORPTION OF WATER BY CELLS

In the performance of their physiological activities, plant cells are continually taking in certain materials and allowing others to pass out. The ability of cells to act in this manner is prerequisite to all other physiological processes of plants. Of the substances which enter and leave plant cells, water is fundamentally important. Water is the liquid in which the colloidal protoplasmic materials are dispersed, it is one of the raw materials converted into foods, it is the liquid in which all solid materials must be dissolved before they can enter or leave a cell or move from one portion of a plant to another, it is the medium in which most of the chemical reactions of living protoplasm occur, and it provides the pressure which is necessary for the maintenance of form, for support, and for the growth of cells. Thus, knowledge of how living cells absorb water is necessary for an understanding of the basic physio-logical processes of plants.

When a cell is in contact with water, the cell wall and the proto-plasm absorb water by a process called **imbibition**. This may be defined as the soaking up of a liquid by solid materials, especially sub-stances in colloidal condition. Imbibition is the phenomenon observed when a dry sponge soaks up water, or when a piece of gelatin or wood is submerged in water. The constituent particles of the solid materials take up the liquid by various physical forces, among which surface

attraction is very important, and as a result of this absorption, the materials increase in volume. Both cell walls and living protoplasm absorb water by imbibition and increase in size as they do so, as may be readily observed in the swelling of seeds placed in water.

The phenomenon of imbibition is sufficient to explain the uptake of water by cell walls of wood and seed coats and other solid, non-living parts of plants, but in the case of living protoplasm, additional forces are involved in the process of absorption. Most of these additional forces are those operative in the physical phenomenon of **diffusion.** Diffusion is defined as the spreading out of the molecules of a substance through all of the space which it can reach, from the place where the substance is most abundant to places where it is less abundant. Diffusion may be regarded as a tendency toward reaching an equilibrium, for it results in the equal distribution within the given space of the diffusing material. For example, when a bottle of ether is opened in a closed room, the molecules of ether, because of their constant motion, move out from the bottle (the place of greater abundance or concentration of ether), and eventually become equally distributed throughout the space inside the bottle and that of the room. If the doors of the room are opened, there is no longer an equal distribution of ether in the available spaces, for the ether-less space outside the room contains zero concentration of ether molecules, while that inside the room possesses numerous equally-scattered particles. Because of their ceaseless vibration and movement, ether molecules will diffuse out through the opened doors, as a result of the difference in their concentration (relative numbers), in accordance with the tendency to reach equilibrium or equalized concentrations. A similar phenomenon occurs when a lump of sugar is dropped into a beaker of water. The sugar slowly dissolves and its molecules move, without being carried by currents, from the surface of the lump (regions of greater concentration) to more remote parts of the water in the cup (regions of lesser concentration of sugar). After a time, the lump of sugar disappears and the sugar particles, having overcome the resistance of the solvent by means of their motion, become equally distributed throughout the surrounding liquid.

Not only does the direction of diffusion of a substance depend upor the relative concentrations of that substance in different places, but the speed of diffusion also depends upon relative concentrations. The greater the difference in the relative amounts of a substance in different plaees, the more rapid is the rate of diffusion from the region of higher concentration to that of lower. Another significant feature of diffusion

is that a diffusing molecule moves independently of other molecules in the available space. If both sugar and salt were added to a beaker of water, the molecules of each of these substances would diffuse until they are equally distributed in the liquid. The rate and direction of diffusion of the molecules of one substance in a mixture of molecules of other substances are ordinarily determined by the concentration of each substance, considered by itself.

If we were to tie over the mouth of the bottle of ether mentioned in a preceding paragraph a membrane which would allow ether molecules to penetrate it, the ether would still continue to diffuse from the bottle into the room, although at a somewhat slower rate. Such diffusion of a substance through a membrane is termed **osmosis**. There exists considerable dispute among scientists as to the exact definition of this term. Physical scientists frequently define it in the broad sense employed above — namely, the diffusion of a liquid, gaseous, or dissolved solid substance through a membrane. Others define it as the diffusion of a liquid through a membrane, and still others, principally certain biologists, interpret the process as the diffusion of water through a membrane. It seems desirable in considering osmosis in relation to living cells, to limit the definition of this process to the diffusion of water through a **differentially permeable membrane**. To understand the essential features of osmosis, the student should bear in mind that the principal force involved is that of diffusion.

A differentially (semi-) permeable membrane is one which allows certain substances to pass through and which prohibits or restricts the passage of others. A membrane of this type is parchment, which permits, for example, the passage of water but prevents the movement through it of sugar dissolved in water. When a membrane prevents such passage, it is said to be **impermeable** to the particular substance which is held back, and **permeable** to the substance which passes through. The cytoplasmic membranes of all living cells are membranes of the differentially permeable type. They allow water, mineral salts and certain other substances to pass through readily, but restrict or prevent the movement through them of certain sugars, pigments, and other materials, especially those of organic nature. The differentially permeable nature of cell membranes is continually changing. Physiological reactions in a cell alter the concentrations of materials within the protoplasm, thus disturbing the equilibrium between materials inside and outside the cell. Changes occur in the acidity or alkalinity of protoplasm, foods are digested or stored, waste materials are formed; these

and other processes influence the differentially permeable condition of the plasma membranes. The state of membrane permeability likewise varies with age, the health and vigor of the protoplasm, and also with various factors in the external environment. Apparently, the permeability of cell membranes may be different simultaneously on opposite sides, and there is some evidence for the belief that the permeability of a cell membrane varies in different parts of the same protoplast at the same time. The fluctuating permeability of the membranes of living protoplasm is attributable to the sensitivity of living matter and to its powers of adjustment to rapidly changing internal and external conditions. In non-living membranes there are no such frequent and continuous alterations of permeability. The effects of a change in the permeability of cell membranes upon protoplasmic contents may be demonstrated by placing a sliced red beet in cold water. The membranes of the beet cells are impermeable to the red pigment and thus prevent its diffusion into the water. The water remains colorless, except for traces of the pigment freed by the cutting of certain cells by the knife. If, however, the beet slices in the water are heated to the death point of protoplasm, the high temperature kills the protoplasm and alters the state of the membranes, which become permeable to most of the red pigment, allowing it to diffuse out of the cells and thus to color the water red.

The basic principles of osmosis may be illustrated most clearly by a simple physical experiment, such as the following. Over the wide end of a funnel a piece of parchment is tightly sealed, in the manner of a drum skin. The funnel is held with the membrane-end down and is partially filled with water through the stem of the funnel. The funnel is then immersed in a beaker of water so that the level of water in the funnel is the same as that in the beaker and the open end of the funnel stands above the water-level of the bowl. Since the relative concentrations of water in the beaker and in the funnel are equal and since the parchment membrane is permeable to the water, molecules will diffuse from the funnel into the beaker and from the beaker into the funnel at the same rate. Thus the volume of the water in the funnel remains constant. If the experiment is repeated, but with the addition of sugar to the water inside the funnel, a different situation obtains. The membrane is impermeable to the sugar but permeable to water. The relative concentrations of water are no longer the same on both sides of the membrane; in identical volumes of the solutions in the funnel and in the beaker, there is relatively less water inside the funnel than there is

in the beaker. The characteristic tendency of diffusion is now apparent — namely, the tendency toward equalization of the concentrations of the diffusing substance on both sides of the membrane. Since the sugar molecules cannot diffuse from the funnel into the beaker and thus reduce the concentration differences between the two solutions, the only manner in which equalization of concentration can be approached is by the diffusion of water from the bowl into the funnel. Water actually moves out of the funnel into the bowl as well as from the bowl into the funnel, but the movement in the latter direction is much greater. This more rapid movement of water from the beaker into the funnel is attributed to the presence of sugar molecules in the solution inside the funnel and to the corresponding reduction of the number of water molecules in contact with the inside of the membrane. In this experiment, there are fewer water molecules in contact with the inner surface of the membrane than with the outer surface of the membrane, for some of the inner surface which might otherwise be in contact with water molecules is occupied by sugar molecules. On the outer surface of the membrane only water molecules are present and thus water passes into the funnel more rapidly than it diffuses out of the funnel. The volume of the solution in the funnel increases as a result of the more rapidly incoming water, and the level of the solution in the funnel rises above that of the water in the bowl. The significant feature here is that, with the passage of water into the sugar solution, the difference in relative concentrations of the water inside the funnel and in the bowl is gradually reduced — in other words, the equilibrium-tendency of diffusion is in large part completed and the rise of the liquid in the funnel becomes slower.

As the volume of water in the funnel increases, the water begins to exert a pressure within the funnel. The volume of water in the funnel continues to increase until the pressure exerted by this water (**hydrostatic pressure**) forces water molecules outward from the funnel through the membrane at the same rate as water molecules enter the funnel from outside the membrane. If, in such an experiment, the membrane is a rigid membrane and is completely permeable to water and impermeable to the dissolved sugar (**solute**) which is on one side of the membrane and if the liquid on the other side of the membrane is pure water, the hydrostatic pressure which develops as described above is termed **osmotic pressure.**

The experiments described above can be repeated, using dissolved materials other than sugar, common salt, for example, so long as the

membrane is impermeable to them, for the relation of the dissolved substance to the relative concentrations of the solvent is a physical one, depending upon the total concentration of dissolved materials, not a chemical one. It should be emphasized that the results of this experiment can be described in either of two ways; we may say that the movement of the water is from the solution of *lesser concentration of dissolved particles* to that of *greater concentration of dissolved particles, OR* we may say that the movement of the water is from the solution of *its* (i.e. the water's) *greater concentration* to that of its *lesser concentration.* Both of these explanations mean actually the same thing, for an *increase* in the number of dissolved particles in a given volume of solution results in a *relative decrease* in the amount of water in proportion to the total volume of the solution. A *decrease* in the number of dissolved particles in a solution results in a *relative increase* in the amount of water in proportion to the total volume of the solution.

There is an analogy between a plant cell and the simple physical experiments described above. In a plant cell, the plasma and vacuolar membranes, with the thin layer of cytoplasm between them behave as a differentially permeable membrane, comparable with the parchment membrane over the funnel. The cell sap is a droplet of water, with various materials, especially sugars and organic acids, dissolved in it. The cell sap is comparable with the sugar solution inside the funnel, for the cell membranes are impermeable to most of the materials dissolved in the cell sap, just as the parchment is impermeable to the sugar in the funnel. Such a cell is in contact with other cells or, if it is an epidermal cell of a root, it is in contact with the water and dissolved materials (**soil solution**) in the soil. The soil solution normally contains a smaller proportion of dissolved materials than does the cell sap; or stated conversely, the soil solution contains proportionately *more* water than does the cell sap. The equalization-tendency of diffusion prevails, and water moves from the place of its *greater* concentration (the place of *lesser* solute concentration) — namely, the soil — into the cell, which is the place of *lesser* water concentration (the place of *greater* solute concentration). Thus the soil solution is roughly comparable with the pure water in the beaker surrounding the funnel in our simple physical experiment. In similar manner, water inside a plant may move from a cell with a relatively high concentration of water (low concentration of solutes) into a cell with a lower concentration of water (higher concentration of solutes). The passage of water from cell to cell or from the soil solution into root cells continues as long as there is a difference

in the relative concentrations of water between cells or between the soil solution and the root cells. The rate at which water moves into a cell depends chiefly on the difference between its concentration inside the cell and outside the cell; the greater the difference, the more rapid the movement. The term **osmotic concentration** is frequently used to indicate the relative amount of dissolved materials to which the cell membranes are impermeable, within the cell sap; a cell with a high osmotic concentration has a large number of such dissolved particles, one with a low osmotic concentration has a smaller number of solute particles in the same volume of solution. A large part of the movement of water from one portion of a plant to another is determined by the varying osmotic concentration of different cells, the direction of water movement generally being from cells with low osmotic concentrations toward cells with higher osmotic concentrations.

It should be emphasized that the comparison between the funnel experiment and the plant cell is a crude one. The same fundamental principle of diffusion is operative in both cases, but the parchment membrane is a non-living membrane with unchanging properties, whereas the membranes of a cell are living and are continually altering in their permeability. The concentration of materials in the cell sap varies from one moment to the next and likewise the concentration of the soil solution or that of adjacent cells continually fluctuates, so that in the absorption of water by living cells, although the basic physical forces of diffusion are at work, their actual operation is conditioned by the temper of the living protoplasm itself.

Plant cells, except when wilting occurs, contain water in such quantity that the protoplasm is forced outward against the cell walls by the pressure of the water in the cell sap. The extent to which the protoplasm can be expanded is of course limited by the surrounding slightly elastic wall of cellulose which can be stretched only so far by this internal pressure. The inwardly exerted cell wall pressure opposes the entrance of further quantities of water after a certain outward pressure of the protoplast against the cell wall has been reached. The water pressure exerted by the cell contents against the cell wall is called **turgor pressure.** Turgor pressure is the actual pressure exerted by the protoplast against the cell wall, while **osmotic pressure,** often used erroneously as a synonym of turgor pressure, is really the maximum pressure which can be developed in the cell sap solution separated from pure water by a rigid membrane which is permeable only to water. The turgor pressure of a cell is usually less, rarely equal to the

actual osmotic pressure which the cell sap might develop under the conditions described in the preceding sentence. The osmotic pressure of the cell sap of some species of plants is as high as 100 atmospheres (1 atmosphere is 15 pounds per sq. in.). In most species of plants, however, the osmotic pressure of the cell sap is less than 15 atmospheres. A cell, the protoplasm of which exhibits turgor pressure, is said to be turgid or to possess turgidity. Turgidity is responsible for the crisp, rigid condition of lettuce leaves or of celery which is immersed in water. When such vegetables wilt, the protoplasts in their cells lose so much of their water that they no longer exert an outward pressure against the cell walls and the tissues become limp, i.e., they lose their turgidity. Turgidity is important in plants in that it aids in the maintenance of form and provides in young cells the pressure which stretches cell walls and thus makes possible the growth in size of such cells. All plant tissues which are well supplied with water and which do not lose water more rapidly by evaporation than they absorb it are normally turgid.

3. PLASMOLYSIS

In accordance with the laws of diffusion, water leaves a plant cell when the relative concentration of water outside the cell becomes less than that inside the cell sap. This is a common phenomenon in the transfer of water from one cell to another. In plant tissues, normally, when water moves from cell to cell, the cell which is losing water is in most cases simultaneously receiving water from some other cell. As a result of this give-and-take, the water supply of a cell is replenished on one side as it is decreased on another side and thus the cell retains its turgidity. If, however, water passes out of a cell toward a region of lesser water concentration and if this outwardly moving water is not replenished, the inevitable result is a loss of volume of the protoplast and its consequent shrinkage. The shrinkage of protoplasm away from the cell wall, due to reduced internal pressure as a result of excessive water loss, is termed **plasmolysis.** Plasmolysis may be demonstrated easily by placing a strip of carrot root or potato tuber in a concentrated salt solution. The relative concentration of water, volume for volume, is less in the concentrated salt solution than it is in the cell sap. As a result of the equilibrium-tendency of diffusion, water passes out from the cells of the potato or carrot into the salt solution, causing a loss of turgidity and the plasmolysis of the cells. The plasmolyzed tissues be-

come very limp. Plasmolysis, if it continues too long, causes the death of the plasmolyzed cells. If, after a short time, however, the plasmolyzed tissues are transferred from the salt solution to pure water, the direction of water movement is reversed, for there is now relatively more water outside the cells than there is inside. Water thus passes inward, the protoplasm increases in volume as the turgor pressure of the cell sap increases, and the tissue regains its turgidity.

The principle of plasmolysis is employed in a number of practical ways. In the making of fruit jellies, usually more sugar is added to the juice than the amount needed to achieve the desired degree of sweetness. This raises the solute content of the jelly (decreases the relative proportion of water) to such an extent that decay and fermentation bacteria, and the reproductive cells of molds falling into the jelly are quickly plasmolyzed, because the water in them diffuses outward toward the region of lesser water concentration, namely into the jelly. Thus, the jelly will not spoil, even though it is exposed to the open air. The addition to meat and fish of quantities of salt fulfills the same object. The organisms of decay which come into contact with the salted foods are plasmolyzed and killed, and thus the meat or fish does not spoil. Another application of the plasmolysis principle is found in the spreading of salt on clay tennis courts or in the cracks of brick walks to kill undesired plants. The seedlings of these plants coming into contact with salt are plasmolyzed in exactly the same manner as the potato slices in salt water are, and the seedlings are thus killed. Pasture weeds, such as the obnoxious Canada Thistle, which are difficult to uproot, are usually destroyed by placing a small quantity of salt about their roots. Plants killed in this manner wilt and turn brown as they die. Because of the wilting and browning of plasmolyzed plants, their manner of death is frequently termed "burning" by farmers and gardeners.

If, in the application of fertilizer salts, excessive amounts are scattered on the soil, the relative concentration of water in the soil solution may become less than that in the cell sap of plants growing in the soil. As a result, the cells of the plant are plasmolyzed and the plants wilt and die unless the excessive quantity of salts is washed away by rain. Thus, the directions given for the spreading of such fertilizer preparations on the soil should be followed implicitly, if the disastrous effects of plasmolysis are to be avoided. If plasmolysis occurs following application of excessive amounts of fertilizer salts, it can frequently be overcome by flooding the soil with large amounts of water.

4. THE ABSORPTION OF SOLUTES

The absorption of dissolved particles by root cells from the soil solution, as well as the absorption of such particles by one cell from an adjacent cell, is a complex phenomenon, not all of the forces of which are known by physiologists. In some cases, the absorption of dissolved materials by plant cells seems to follow the basic law of diffusion — namely, the molecules of a dissolved substance diffuse from the region of their greater concentration toward a region of their lesser concentration. In absorption as a result of simple diffusion, the molecules or **ions** (electrically charged particles into which many types of molecules dissociate when they are in solution) move into a plant cell, for example, an epidermal cell of a root, only when the concentration of those particles is *greater* outside the cell than it is inside the cell. The continuation of such absorption obviously depends upon the maintenance of a concentration gradient (difference) of the particles of the diffusing substance; entry of these particles into a cell continues only so long as the particles are present in greater concentration outside the cell than in.

Apparently, however, the absorption of solutes by living plant cells sometimes involves much more complex phenomenon than simple diffusion. There is abundant evidence which indicates that the molecules and ions of many substances continue to diffuse into plant cells even when the ions and molecules of these substances occur in greater concentration within the cells than they do outside. In other words, such movement is in a direction opposite to that which would be maintained in the case of simple diffusion. This movement of solute particles from a region of lesser concentration (e.g., soil solution) toward a region of greater concentration of these particles (e.g., a root epidermal cell) appears to be a rather common phenomenon in the absorption of solutes by living plant cells. It has been known for many years, for example, that certain marine algae are able to accumulate within their cells large concentrations of iodine, which occurs in exceedingly minute quantities in sea water. Despite the fact that the concentration of iodine is much lower in the sea water than it is in the tissues of the algae, the absorption of iodine by the algal cells continues. A similar type of behavior is apparently involved in the absorption of many other kinds of solutes by plant cells.

This **active absorption,** as it is frequently called to distinguish it from the type of absorption which results from simple diffusion, seemingly

occurs as a result of the expenditure of energy by living protoplasm. Such accumulation of solutes against a concentration gradient ordinarily occurs only when oxygen and carbohydrates (sugars) are present, and thus seems to be dependent upon the rate of respiration and energy release in the absorbing cells. It is likely that the attraction (**adsorption**) of protoplasmic colloids for certain ions is another of the several forces involved in the active absorption of solutes. Thus the process of active absorption is appropriately named, for it appears that the protoplasm of living cells actually furnishes the energy and the colloidal attraction which the absorption of solutes in this manner requires.

From the soil, plants absorb various substances, chief of which are mineral salts, the raw materials from which certain kinds of food and other organic products are manufactured by green plants. Most important of the mineral salts taken in by plants are sulfates, nitrates, and phosphates, to which the membranes of plant cells are permeable. Only materials to which cell membranes are permeable and which are dissolved in water can enter plant cells. These solutes may enter plant cells in either molecular or ionic form. Those substances (e.g., mineral salts), the molecules of which freely dissociate into ions in solution, are absorbed chiefly in ionic form, whereas those substances whose molecules do not dissociate and which enter living cells, must obviously be absorbed in molecular form. The molecules of the important mineral salts of the soil, for example, magnesium sulfate, potassium nitrate, calcium phosphate, and others — dissociate freely in the soil solution and apparently enter the absorbing cells of roots chiefly as ions. Magnesium sulfate molecules dissociate into magnesium and sulfate ions, calcium phosphate into calcium and phosphate ions, etc.

Another of the important features of the absorption of mineral salts is the fact that the entrance of any given solutes into a cell is usually independent of the absorption of other solutes, although there is some evidence to show that the concentrations in which certain ions are present tend to influence the rate at which other ions are absorbed. It is an interesting fact that as certain ions enter living plant cells, other ions may be simultaneously diffusing out of the same cells. Thus, ions are not swept into plant cells as a result of the mass movement of water, but move in a more or less independent fashion which is determined by a variety of complex, only partly understood factors.

In the preceding sections, it was emphasized that the total concentration of dissolved materials in the cell sap of cells is usually greater

than the total concentration of solutes in the soil solution. In this section, it has been implied that the concentration of the individual soil salts may be normally higher in the soil solution than it is in the cell sap of root cells. These statements may seem somewhat contradictory, until it is pointed out that, although the concentration of mineral salts may be lower in the cell sap than in the soil, the *total* concentration of dissolved materials is nevertheless greater in the cell sap than in the soil, principally because of dissolved sugars and other organic materials in the cell sap. The sugars and related materials, to which the cell membranes are rather impermeable, rather than mineral salts, are the more important osmotically active substances of plant cells.

Another question which may logically be raised here is: if the membranes of plant cells are impermeable to sugars and other organic substances, how is it that these materials are able to move from one part of a plant to another? The answer to this is to be sought in the fact that the permeability of these membranes varies from time to time and that these membranes are not completely impermeable to many of these substances. Thus, as permeability conditions change, some of the sugars and other materials dissolved in the cell sap and protoplasm may diffuse outward from certain cells and enter other cells.

5. THE FORMATION OF NEW CELLS

It was mentioned in the first chapter that one of the fundamental attributes of living protoplasm is its ability to grow. Growth is a complex process which is the culmination of many other processes in plants — the intake of water and mineral salts, the manufacture of food, the secretion of cellulose into cell walls, the assimilation of proteins into living protoplasm, and others. The first stage of growth in living organisms is the formation of new cells by a process known as **cell division,** which occurs most commonly in the meristematic tissues of plants: the growth tissues at the tips of roots and stems, the cambium, cork cambium, and others. Following cell-division, the newly-formed cells undergo enlargement and differentiation processes to be discussed in a subsequent chapter.

The process of cell-division proceeds in two phases, first, the division of the nucleus of the parent cell into usually 2 nuclei, each of which becomes the nucleus of one of the new cells formed, and second, the subsequent formation of a new cell wall separating the nuclei and
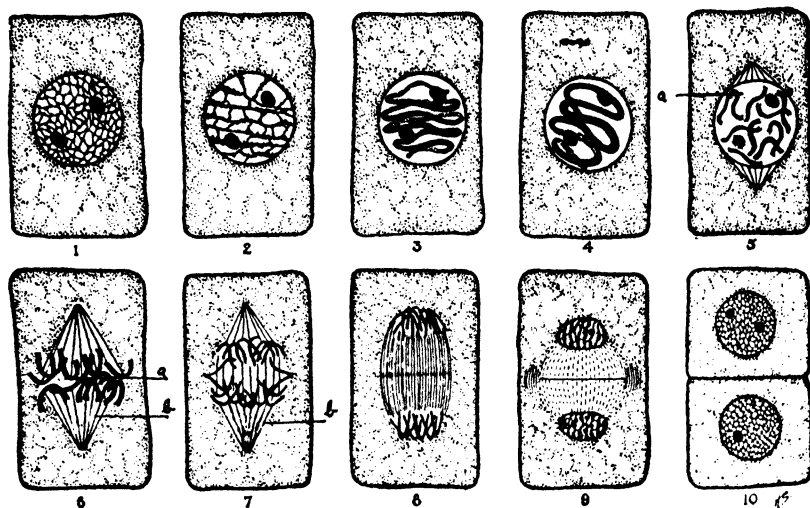
Fig. 12. Stages in plant mitosis

1. Resting cell.	7. Anaphase.	10. Daughter cells.
2-5. Prophase.	8. Telophase.	a. chromosomes.
6. Metaphase.	9. Cell-plate stage.	b. spindle.

dividing the original cell into 2 new cells. In the cells of some plants, several divisions of the nucleus occur without the formation of new walls; this results in cells with more than one nucleus, a condition found chiefly in certain species of thallophytes. In higher types of plants, however, each cell usually has one nucleus, and when cell division occurs, two cells, each with a single nucleus, are formed.

The nucleus contains chromatin, the controller of hereditary traits, which is exactly divided qualitatively and quantitatively so that the newly-formed cells (termed **daughter cells**) have the same hereditary characteristics and potentialities as the parent cell (**mother cell**). The exact distribution of the hereditary material of the nucleus is achieved by a complex process called **mitosis** (Figure 12), a process which is quite similar in both plant and animal cells. For the sake of convenience in studying mitosis, biologists usually divide the process into a number of **phases** (Figures 13, 14), each of which bears a technical name. Actually the process of mitosis is a continuous one with no distinctly marked stages. These "phases" are thus comparable with the moon's "phases," which gradually merge into each other.

In a nucleus which is not in the process of mitosis (**resting nucleus**),
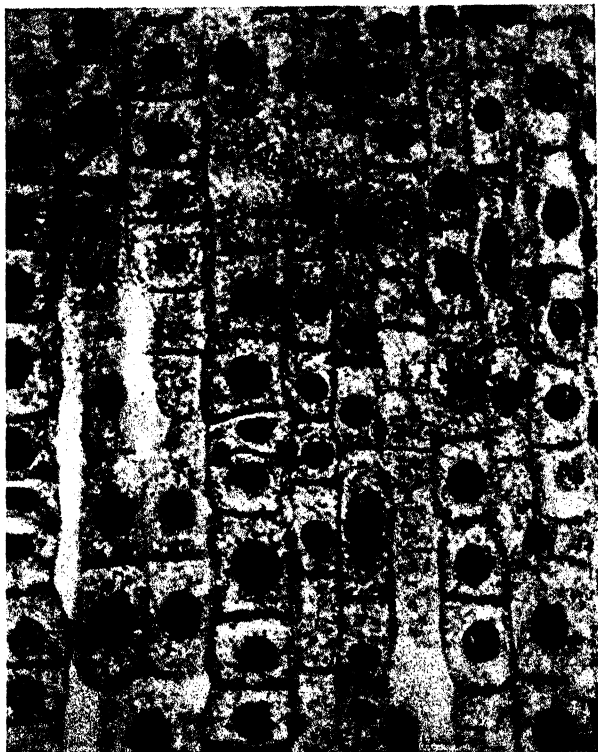
Fig. 13. Photomicrograph of a portion of the embryonic tissue of a root tip, showing various stages in mitosis.

Photo by Triarch Botanical Products

the chromatin material appears somewhat granular after the application of certain dyes to make it visible, and frequently is distributed in the form of a diffuse, irregular network. When mitosis begins, the chromatin network separates into rod-like bodies, the **chromosomes,** chiefly by the disappearance of connecting strands among the denser parts of the net. In a few species, the chromatin apparently condenses into a long, continuous, coiled thread, the **spireme,** which then splits transversely into a number of segments, the chromosomes. At the same time, at opposite ends of the nucleus, **fibers** appear in the cytoplasm and begin to grow towards each other. During the formation of these fibers, the nuclear membrane and the nucleolus disappear. The stages of mitosis through the disappearance of the nuclear membrane are included in the term **prophase.** During the late prophase longitudinal splits occur in the chromosomes. Following the disappearance of the nuclear membrane, the fibers form a somewhat ellipsoidal, tapering **spindle** with the fibers radiating inward from the opposite ends or

poles of the spindle. There are two kinds of fibers in the spindle, some which extend from the poles to the chromosomes, to which these fibers are attached, and others which extend from pole to pole. There are two bundles of fibers attached to each pair of chromosomes, one on one side of the longitudinal split, the other fiber to the other half of the same chromosome. The chromosomes become arranged in the central plane of the spindle at right angles to its longitudinal axis. In the **metaphase** of mitosis, the halves of the equatorially-situated chromosomes begin to separate so that at the end of the metaphase there are twice as many chromosomes as there were when the splitting process began. This process completed, the separated halves of each chromosome then move toward opposite poles of the spindle, seemingly as a result of spindle-fiber contraction. Sometimes these fibers are attached near one end of the chromosomes, as a result of which the chromosomes appear crook-shaped as they are pulled by the fibers. More frequently, the fibers are attached near the middle, resulting in the formation of U-shaped chromosomes. The stage of mitosis during which the two sets of chromosomes are moving in opposite directions is called the **anaphase**. Each of these sets is composed of the longitudinally split halves of the chromosomes of the parent nucleus and are thus of the same kind and number as those of the parent cell. Each chromosome bears in linear arrangement a number of hereditary determiners, or **genes**, each of which is split when the whole chromosome undergoes longitudinal splitting. Thus when a chromosome separates into two chromosomes, two sets of identical genes are produced, one set in each chromosome. The relation of genes to hereditary phenomena will be discussed in a subsequent chapter.

The two groups of chromosomes reach opposite ends of the spindle and the organization of two new nuclei begins. This last step in mitosis is called the **telophase**. In this stage, the chromosomes seem to lose their individuality, and swell to re-form the characteristic network of the resting nucleus. The spindle-fibers disappear and the nuclear membrane and nucleolus are formed. During the telophase the formation of a new wall across the cell in the central region of the spindle between the reorganizing nuclei begins. This new wall is soon completed and thus there are two cells, each with its own nucleus, which have been formed from the protoplasm of the original cell. Each of the newly-formed cells is about half the size of the parent cell at the time of completion of the new wall. These daughter cells then enlarge, as a result of the formation of additional protoplasm and the growth of the cell
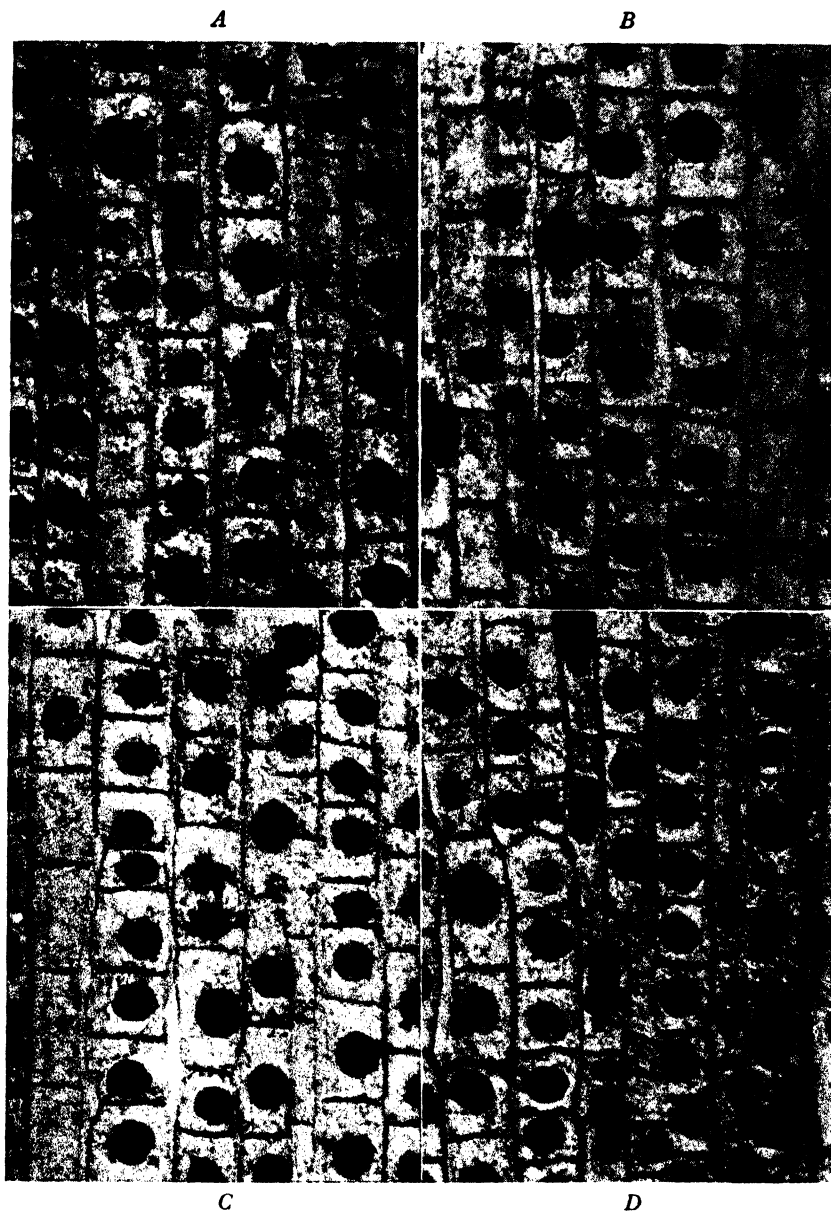
Fig. 14. Photomicrographs showing mitosis in cells of onion root tips

A. Shows cell-plate stage (upper left) and metaphase (lower center). B. Shows early prophase (left center) and anaphase (lower center). C. Shows telophase (center). D. Shows cell-plate stage (lower center).

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walls, until they reach a size about equal to that of the mother cell. When they reach this size, if they are still in embryonic condition, they may in turn undergo mitosis and cell division, or they may become differentiated into mature cells of the plant.

This complex process of insuring the equal distribution of chromatin from mother cell to daughter cells requires varying periods of time in different species of plants and under varying external conditions. In most cases the process is completed within a period of 45 minutes to slightly more than an hour.

The spindle "fibers" are probably not fibers in the sense in which this word is ordinarily used. Rather, they are usually considered to be colloidal materials in a gel state, or if in a sol condition, of a greater viscosity than the remainder of the cytoplasm. Physico-chemical changes in these colloidal materials induce the contractions which draw the chromosomes towards the ends of the spindle.

Chromosomes are of interest because of their individuality. Each species of plant and animal has a certain number of chromosomes in all of its cells, except sexual reproductive cells (and frequently certain other cells which are involved indirectly in sex-cell production) which have half the number of chromosomes of the body cells. The body cells of onion plants, for example, have 16 chromosomes, those of tobacco 48, those of maize, or corn, 20, and so on. Not only are the chromosomes individualistic with respect to their numbers, but also with regard to their structure. For example, there is usually the same number of crook-shaped chromosomes, the same number of U-shaped chromosomes, etc., in the chromosomes of every body cell of all the ordinary plants of a given species. The behavior and organization of chromosomes will be discussed in detail in a later chapter on inheritance.

6. OTHER PHYSIOLOGICAL PROCESSES OF CELLS

In addition to the processes of absorption and of cell division, many other physiological processes occur in plant cells — processes of food manufacture, digestion, respiration, assimilation, etc. Since these are most satisfactorily studied in the light of the basic processes of food manufacture and since food manufacture is most satisfactorily studied in conjunction with the study of leaf structure, these functions will be considered after a discussion of leaf morphology. All these physiological processes are physico-chemical in nature.

SUMMARY

1. Protoplasm is a complex colloidal system, capable of many kinds of chemical reactions.

2. The most abundant chemical elements in protoplasm are carbon, hydrogen, oxygen, and nitrogen, which constitute between 95 and 98% of protoplasm.

3. The remaining 2 to 5% of protoplasm is made up of or contains sulfur, calcium, phosphorus, potassium, iron, magnesium, and other elements, including manganese, boron, copper, aluminum, and others.

4. Plant cells absorb many kinds of dissolved substances from the soil or other medium. Some of these solutes are essential to normal growth, others have apparently no value in plant growth and may even be injurious.

5. These chemical elements do not occur in elemental form in protoplasm, but are combined into chemical compounds. Most abundant of these compounds in living protoplasm are proteins, less abundant are fats, carbohydrates and other compounds.

6. Many of the compounds found in protoplasm are not parts of the living substance but are waste-products, energy-supplying substances, etc.

7. It is impossible to classify the compounds in protoplasm as living or non-living. The organized system of protoplasm is alive, not its individual constituent compounds.

8. Plant cells absorb water by imbibition and osmosis. Imbibition is the soaking up of a liquid by solid materials, especially materials in colloidal condition. Both cell walls and protoplasm absorb water by imbibition.

9. Osmosis is the diffusion of water through a differentially permeable membrane from a region of high water concentration to a region of lower water concentration.

10. Cytoplasmic membranes are differentially permeable, and vacuoles are droplets of water with considerable quantities of dissolved substances — sugars, salts, etc. Cytoplasmic membranes and vacuoles are directly involved in the osmotic process of water absorption by protoplasm.

11. When the protoplasm of a cell contains such quantities of water that it exerts an outward pressure against the enclosing wall, it is said to be turgid.

12. Plasmolysis is the shrinkage of protoplasm away from the cell wall due to the outward diffusion of water from protoplasm.

13. Plant cells absorb solutes chiefly by a process of active absorption in which living protoplasm actively absorbs solute particles (chiefly ions) against a concentration gradient. Active absorption apparently involves the expenditure of energy by protoplasm, as well as other forces not fully understood.

14. The formation of new cells results from the division of pre-existing cells. In most cells, this process of cell division immediately follows a process of nuclear division (mitosis) in which the dispersed chromatin of the nucleus is organized into chromosomes, which split longitudinally and are separated. Mitosis results in the qualitatively and quantitatively equal division of the hereditary substance, chromatin, between the newly-formed cells.

15. The number of chromosomes is usually constant in all the body cells of plants of the same kind. Chromosomes are also individualistic in their form and structure.

16. Other physiological processes which go on in living cells are food manufacture, digestion, respiration, assimilation, etc.

Roots and the Relation of Plants to the Soil

THROUGH THEIR root systems, plants are in close contact with the soil. The roots of most plants are subterranean and thus are not visible above the surface of the ground. The principal functions of roots are the absorption of water and dissoved mineral salts from the soil, the firm anchorage of plants in the soil, the conduction of the absorbed materials up into the stem, the transfer of foods manufactured in the leaves downward into the growth and storage regions of roots, and in the roots of many plants, the storage of food.

1. SOILS

There are many types of soil in which plants grow. They vary in their origin, the nature of their chemical constituents, their physical properties, their depth, and in other respects. Although the variations in these qualities are extreme among the many types of soil on the surface of the earth, there are certain characteristics common to soils. All soils are complex mixtures of particles of various sizes, they contain some materials which are soluble in water and other materials which are not, and they contain air in varying quantities. There are certain kinds of materials present in most soils, at least in those which support the growth of plants. These substances are rock particles, air, water, soluble inorganic chemical compounds, organic matter, and living organisms.

The air content of soils is exceedingly important because one of the principal components of air is oxygen which is essential for the normal respiration and growth of the roots of most species of plants. The amount of air varies in different types of soils and with certain environmental conditions. In soils, such as clay, which are composed of small, tightly-packed particles, there is less air space present than in soils of the

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loam types; in soils, if the spaces between soil particles are filled with water, as they are during heavy rains or if water stands in them because of poor drainage, the air is forced out of these spaces. Such soils are described as **water-logged**. In clays and certain other types of soils a large amount of the materials present exists as colloidal particles which hold water very tenaciously. Thus clay soils after a heavy rain may remain in a near-water-logged state for longer periods of time than soils in which colloidal materials are not so abundant and from which water drains away more rapidly. The growth of many kinds of plants is exceedingly difficult in clay soils in part because of the relatively low air content of such soils. In most types of field and garden soils, air spaces make up from 20% to 40% of the total soil volume, a sufficient amount to ensure the normal root development of most cultivated plants. The ideal condition for plant growth obtains when the soil particles contain, or are covered by, adequate supplies of water and when the spaces among these particles are free of excess water and thus contain air. One of the principal benefits of cultivating soils is the agitation and separation of soil particles and the concomitant increase in the relative air space of the cultivated soil.

The quantity of water in soils is determined by a number of factors, chief among which are the amount of rainfall, the water-holding qualities of the particles present, the nature of the subsoil, with reference to the rapidity of drainage, and the degree of slope of the soil surface. A large proportion of water falling as rain flows away over the surface of the soil as **run-off** water. This water is valueless in the growth of plants for it does not penetrate the soil. The greater the slope, the more rapid is the rate of run-off, and the greater is the degree of soil erosion by the moving water. The remainder of the water enters the soil. A portion of this is held in thin surface films by many of the soil particles; this surface film water, together with that held in the interstices of soil particles, is termed **capillary water,** since the force which is largely responsible for its being held is the force of surface attraction, or **capillary force**. It is principally the capillary water of soils which is available for absorption by the roots of plants. The remainder of the water which enters the soil percolates downward through the soil particles to the **water table,** or standing water, the depth of which varies in different types of soils, and in different regions. This percolating or **gravitational water** is unavailable to plants, except as it percolates through the layers of soil in which roots are present, for the **water table** is usually at a level below the maximum depth reached by most roots.

When the capillary water at the surface of the soil evaporates, water from sub-surface particles moves upward by capillary attraction of the surface particles and thus moistens them. In a protracted dry period, a large part of the capillary water in a soil may rise to the soil surface in this fashion and evaporate. The height to which water will rise by this surface force or capillary action is greater when the soil particles are small and are close together than when they are large and separated, for there is more surface area exposed by small particles in proportion to their volume than there is by larger particles, and the movement of water from particle to particle is facilitated by contiguous surfaces and surface attraction. In certain soils, this capillary rise may occur through a height of several feet. If the water table is high, a portion of the gravitational water may rise by this capillary force into the upper layers of soil, as they suffer drying. In many soils, however, the water table is too deep for its water to rise to the topsoil by capillary action. One of the benefits of frequent cultivation of the soil lies in the fact that such treatment keeps the soil particles separated and prevents their packing, thus conserving the capillary moisture in the soil, for capillary movement toward the surface of the soil is promoted by the close contact of soil particles. This practice is made use of in **dry-farming,** a type of agriculture common in many parts of the western United States, in which the rainfall is rather scanty, that is, between 10 and 20 inches a year. In dry-farming, the upper portion of the soil is cultivated continuously after rains to keep the upper soil particles from compacting and thus to decrease capillary rise in the top layer of soil. Water may rise by capillary action from deeper layers of soil into the layers within which the roots of crop plants grow, but the continuous plowing of the uppermost soil layer and the consequent reduction of capillary rise in this layer conserve the moisture in the underlying layers. Another method of reducing the capillary rise of water and the accompanying surface evaporation is the process of **mulching.** A mulch is a layer of material spread over the surface of the soil to screen it from the drying action of wind and sun, and thus to conserve moisture, and also to prevent the growth of weeds. Common mulching materials are dead leaves, straw, and manure. Recently the use of glass-wool and of cheap grades of paper as a mulch has appeared; in Hawaii, for example, layers of paper are employed as a mulch around pineapple plants.

Even after the complete evaporation from soil of capillary water, there remains a small amount of water which is held very tenaciously

by the smaller soil particles, particularly those of colloidal nature. This **hygroscopic water** cannot be readily removed from these particles by roots and consequently it is of little importance as a water source for plants.

Rock particles form the largest proportion of all the materials in most soils. These particles vary in size from very small diameters in clay to large diameters in coarse sands and gravel. The various types of loam soils have particles lying between these extremes of size. These particles develop from the decomposition of rock by the action of running or dripping water, alternate freezing and thawing, winds, the grinding action of glaciers, and the disintegrating action of the carbon dioxide (carbonic acid) secreted by the roots of plants. Some rock particles, chiefly those transported by glaciers and those washed by swift-flowing streams are rounded, whereas others are quite angular with sharp points and flat surfaces. The presence and character of rock particles are of importance in determining in a large degree the proportion of air space in the soil, the amount of capillary water held by the soil particles, the rapidity of percolation of the gravitational water and other physical features of solids. Rock particles are also important in that their further disintegration results in the formation of some of the soluble mineral salts of the soil, which are absorbed and used by plants.

The mineral salts — particularly nitrates, phosphates and sulfates — are the most important of the dissolved inorganic materials of soils. They constitute the chief raw materials which plants absorb from the soil and synthesize into foods, chlorophyll, and other organic materials. These substances, together with numerous other dissolved materials, as has been pointed out before, are absorbed by the roots of plants, as a result of processes of diffusion and of active absorption.

Organic matter — that is, the material derived from the waste products of living organisms and from the decomposition of the dead bodies of plants and animals — occurs in all soils in which plants grow and in or on which animals live. Certain types of soils, such as recently formed volcanic soils, and soils consisting almost entirely of sand and gravel, possess little or no organic matter. The greater part of the organic substance of soils is of plant origin, chiefly from the dead root systems of plants and from fallen leaves. The organic chemical compounds — cellulose, proteins, and others — are decomposed by various species of bacteria, and other organisms, and are ultimately reduced to simpler inorganic compounds in the soil such as ammonia and other

nitrogen compounds, phosphates, water, carbon dioxide, etc. The partially decomposed, usually dark-colored organic materials of soils are very important in the growth and development of plants rooted in the soil. The disintegration of these organic materials produces and maintains in the soil a continuous supply of inorganic substances which higher plants require. Thus organic compounds are important in continued soil fertility. Furthermore, organic substances constitute the chief food of various types of bacteria which are necessary to keep soils fertile. Most organic materials of the kinds found in soil are able to imbibe and hold water with great force, and because of their somewhat spongy nature, are able to loosen the soil and thus to prevent the formation of heavy crusts and to increase the proportion of air spaces in the soil. The supply of organic matter in cultivated soils can be kept constant or increased by the addition of manure and also by the cultivation and subsequent plowing under of certain crops, especially nitrogen-capturing crops such as alfalfa, clovers, soy-beans, and others. This latter process is sometimes called "green-manuring." All dead plants as they decompose increase the nitrogen content of soils; legumes are especially effective in this activity because their roots contain nitrogen-fixing bacteria which convert free, atmospheric nitrogen into nitrogen compounds in the soil.

A considerable portion of the substances present in many kinds of soil exists in a colloidal condition, particularly in loam and clay soils. Various organic materials which accumulate following the decomposition of dead plant and animal tissues, as well as certain inorganic mineral compounds (e.g., aluminum and silicon compounds) are commonly found in intricate colloidal systems in soils. That such materials exist in colloidal states is important in the relationships between plant roots and soils. These colloidal substances increase the water-holding ability of the soil, and their powers of surface attraction, as well as the frequent instability of such systems, are important in the complex processes of ion exchange and of the absorption of various ions by the surface cells of roots.

It is perhaps debatable whether the organisms which inhabit the soil should be considered as actual constituents of soil. Generally they are regarded as such, for they are present in most kinds of soils, at least those in which there is some organic matter, and they exert important influences upon the physical and chemical properties of soils. Among the organisms which pass all or a portion of their lives in the soil are insects, worms, mice, and other rodents, and various fungi, most com-

mon of which are bacteria. The animals excrete waste products which
enrich the nitrogen stores of soils and they influence the physical
nature of soils by continually stirring up the soil particles. Most signif-
icant of all these organisms with respect to chemical transformation
in the soil are bacteria, of which there are several species present in
soils. Some of the bacteria decompose the complex organic compounds
of the dead bodies and excretions of plants and animals, and thus in-
crease the supply of simpler inorganic compounds in the soil, other
species are able to take nitrogen gas from the air and convert it into
nitrogenous compounds in their bodies, compounds which can later
be used by green plants. The various kinds of soil bacteria are involved
chiefly in the chemical activities and transformations of nitrogenous
substances in the soil. Nitrogen is one of the most important chemical
elements concerned in plant nutrition and its presence in soil in usable
forms is necessary for the normal development of green plants. Without
the activities of bacteria, the supplies of available nitrogen compounds
in the soil would soon be depleted, as a consequence of which the
growth of green plants would cease. The relations of bacteria to the
nitrogenous substances of soils is quite complex and will be discussed
later in the chapter on bacteria.

2. HOW PLANTS INFLUENCE SOILS

There are three general ways in which plants influence the soils in
which they are growing: they take from soils water, mineral salts and
other substances, they add materials to soil as a result of processes of
excretion and of the decomposition of their dead portions, such as
fallen leaves, dead roots, etc., and they influence the physical nature of
the soil by means of their roots, which penetrate the soil and thus make
it looser and more porous and which hold the soil firmly against forces
of erosion.

All green plants absorb sulfates, phosphates, nitrates, and other
materials from the soil, different species absorbing these substances in
different quantities. If plants continue to live on the same soil year
after year, their falling leaves, dying roots, and decaying branches
return through bacterial action most of these raw materials to the soil,
so that there is a continuous supply of such substances available. A
different situation obtains, however, on soils which are intensively
cultivated. Seeds are planted and the resulting plants are harvested
when they are mature for the edible fruits, leaves, stems, or roots which

they produce. Since there are bound up in these products chemical elements taken in by roots, the harvesting of such crops depletes the raw materials of the soil. If no provision is made to restore such substances after each harvest, soils soon become incapable of supporting adequately the further growth of plants. Such soils, we say, have lost their fertility. In the eighteenth and nineteenth centuries in the United States, pioneers in the Middle West, and Far West, and South, frequently cultivated crops on a certain patch of soil until the raw materials of the soil became depleted, then moved on to fresh lands, a practice which was much easier at that time than restoring the fertility of the soil by adding needed fertilizers. As a result of such mistreatment, many soils were exhausted to such an extent that many years have been required for restoration of their fertility. The fertility of cultivated soils may be maintained in part by plowing under the stubble, dead leaves, and other waste portions of harvested crops, by adding minerals and organic matter in the form of commercial fertilizers and manures to soils, and by crop rotation. Since different species of plants take substances from soils in different quantities and since they likewise add to soils substances of different kinds in varying amounts, the culture of different crops on the same soil in successive years tends to reduce the possibility of complete exhaustion of certain mineral elements and to add to soils diverse materials, the decomposition of which makes up in part for the withdrawal of substances by plant roots.

Plants differ from most animals in that they do not possess excretory systems for elimination of waste products. Waste products of plant metabolism are usually stored in certain out-of-the-way tissues, such as the heartwood of trees, portions of the outer bark, etc. Some of these products, however, are not retained within the plant body, but diffuse out into the soil from roots. Most common of these root excretions is carbon dioxide, one of the products of plant respiration. Carbon dioxide may accumulate in soils with poor drainage, often to the extent of stunting the very roots which produce it. Carbon dioxide dissolves in water to form a weak acid, carbonic acid, which attacks and slowly disintegrates certain types of rock particles, particularly carbonates. One of the classic experiments in plant physiology is the growth of plants in such a manner that their roots are in contact with polished marble blocks. After several days or weeks of growth, the polished surfaces of the marble show etched lines coinciding with the position of the roots on the blocks. The carbon dioxide excreted by plant roots, then, is an important factor in bringing about the disintegration of

rock particles in soils. The roots of some plants apparently excrete other materials in addition to carbon dioxide. These materials are possibly organic acids, which are frequently inimical to root growth. Walnut trees have been observed to stunt the growth of certain other plants growing within the range of their roots. The growth of blue-grass is frequently poor near walnut trees and the injury and death of apple trees in the proximity of large walnut trees have been reported. There is some doubt as to whether the harmful effects of walnut trees on other plants is attributable to the excretions of waste products by their living roots, or to the products of decomposition of dead roots, bark, etc., of this species. In either case, the roots of plants in their normal growth do add materials to soils, whether in the form of excretions from living roots, or in the form of products of the decay of dead portions of root systems. The amount of oxygen in the soil is involved in the accumulation of such organic waste products. In well-drained soils with large amounts of air space, waste products of roots do not accumulate in the large quantities that they frequently do in poorly aerated soils. The developments of these waste products in the soil is doubtless another of the reasons in favor of crop rotation for it seems that the root wastes of the plants of a certain species are frequently more deleterious to other plants of the same species than they are to plants of other species.

The numerous ramifications of roots growing through the soil tend to keep the soil relatively open and loose, not only because of the organic matter left by dead roots, but also because of the direct mechanical effects of roots in penetrating and breaking hard lumps of soil and hard soil layers. The roots of many plants, particularly those plants, such as grasses, which form dense sods, are also significant in that they hold soils in place and reduce or prevent erosion. The chief reason for the present widespread soil erosion by the action of wind and water on the watersheds of our major rivers and in the dust-bowl areas of the Southwest, has been the thoughtless destruction of the plant cover. Dense forests have vast branching systems beneath the soil, as well as above it, systems which bind the soil and keep it in place. The undergrowth of forest — shrubs, mosses and other small plants — also aid in the retention of soil. When forests are destroyed, their roots die, and thus can no longer hold the soil. The plants of the forest floor, unable to stand the direct sunlight admitted to them by the cutting away of the trees, likewise perish and thus lose their ability as soil binders. Plants prevent erosion, not only because their roots hold the soil in place in a physical manner, but also because they take in and

use large amounts of the rain which falls on them, and because their aerial portions reduce appreciably the force of raindrops and also of winds before they strike the soil. Most effective in preventing soil erosion are sods, formed chiefly of grasses. These sods form extensive coverings on the soil, protecting it from the action of both wind and water. In regions of strong winds, such as in the Southwest, the destruction of the sod to create farm land has exposed the topsoil to the winds, which have carried it away by the hundreds and thousands of tons. Attempts to restore the sod on such soils in an effort to check the erosion frequently fail because the unceasing winds agitate the soil continually, thus making it very difficult for grass seedlings to establish themselves and to re-form the sod. One of the most important programs of governmental conservation agencies at present is the campaign to inform the public of the grave dangers of soil erosion and to reclaim the vast, badly eroded areas of our country by scientific replanting with soil-holding plants and the subsequent proper care of such vegetation.

3. THE ORIGIN AND GROSS STRUCTURE OF ROOTS

A seed contains a miniature, rudimentary plant, known as the **embryo**, which develops into a mature plant after the seed germinates and the embryo grows. A portion of the embryo, the root primordium (**radicle**) at the lower end of the **hypocotyl** is usually the first structure to emerge from the seed when the seed germinates. The first root is termed the **primary root.** The primary root begins to produce branches before it is many days old; these branches in turn give rise to branches of their own. These various branches of the primary root are called **secondary roots.** The primary root usually grows straight downward whereas the secondary roots grow out at first in somewhat horizontal position and may later turn downward near their tips. Sometimes roots are produced on stems or on various types of leaves; roots of this type, which arise from some structure other than the original hypocotyl or primary root, or one of its branches, are termed **adventitious** roots (Figure 15). The aerial roots of poison ivy which attach the stems of this vine to a solid support, the roots which grow from bulbs and other kinds of underground stems, and the roots which develop from stem cuttings of roses, geraniums and other plants are examples of adventitious roots. The vegetative propagation of plants from stem cuttings or from leaves is made possible by the ability of such parts of the plant
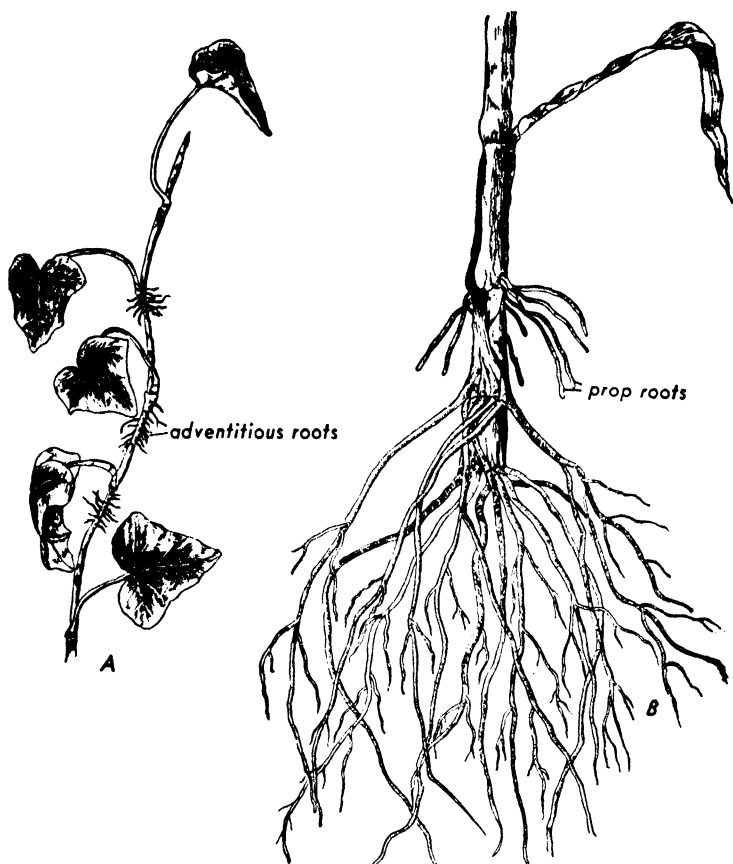
From Plant Life *by Wilson and Haber*

FIG. 15. Adventitious roots. *A.* Of English ivy. *B.* Prop roots of corn.

body to form adventitious roots. The prop roots of corn and other cereals, which arise from the stem joints at or above the surface of the soil and grow downward into the soil, sometimes form the principal portion of the root systems of such plants (Figure 22).

The entire mass of subterranean roots produced by a plant is called its **root system.** The degree of branching, depth of penetration into the soil, the extent of horizontal spreading of branches, and other properties of root systems vary in different species of plants. Botanists distinguish between two common types of root systems: **diffuse (fibrous) root systems** (Figure 16) and **taproot systems** (Figures 17, 18).

Diffuse root systems are composed of numerous rather slender roots,

the main ones of which are of nearly equal size. Diffuse root systems are often entirely adventitious in origin, as in corn and other grasses, in which the primary root fails to continue its growth and is replaced by a number of adventitious roots, the largest ones of which are nearly alike in size. In other plants with diffuse root systems, the primary root may develop a number of secondary roots which grow more rapidly than it does, and ultimately constitute the main part of the root system. Roots of this type are, of course, not adventitious, since they arise as branches of the primary root. Diffuse roots often remain slender, as in corn and other grasses, in which case they are termed **fibrous roots** (Figure 19). In such plants as the sweet potato and dahlia, the larger diffuse roots become swollen with stored food; such roots are called **fleshy diffuse roots.** In many trees the diffuse roots become woody after years of growth. A taproot system is one in which the primary root grows most rapidly and remains the largest root, with a number of smaller secondary roots. Root systems of this kind are found in beets, dandelions, and radishes. As in the case of diffuse roots, some taproots may be slender, some may be fleshy, and others woody.
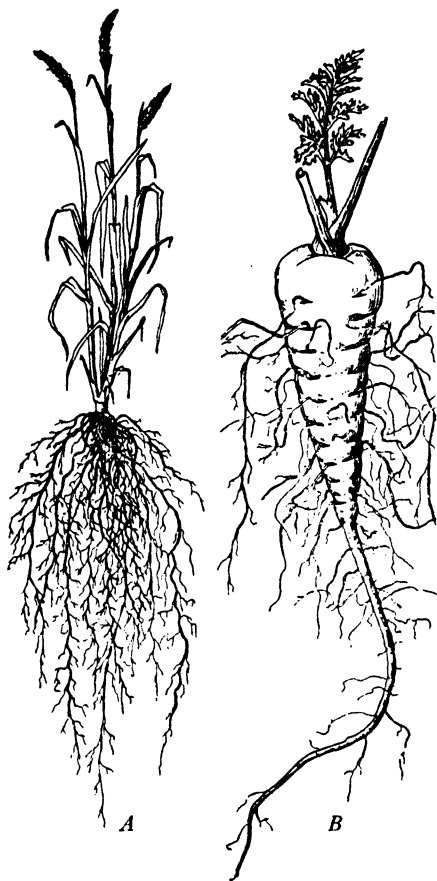
Fig. 16. Root systems

A. Fibrous root system of a grass.
B. Taproot system of a carrot.

The form of root systems and the depth of their penetration into the soil vary with different species and with different factors in the soil. Each species of plant has, as a rule, a certain characteristic form of root system, and often a preferred depth of growth. Both of these features,

Fig. 17. Storage taproot of wild sweet   Fig. 18. Taproot of hickory tree.
potato (*Ipomoea*). Length — 9 feet. Greatest
diameter — 1 foot.

particularly the latter, however, are susceptible to the formative effects
of the soil. In many types of plants, particularly herbs, the length of
the mature roots is often greater than the height of the stem above
ground. In wheat plants, for example, the stem usually reaches a maxi-
mum height of 3 to 4 feet, whereas the roots have been found to pene-
trate 9 feet or more into the soil. Other plants with deep root systems are
alfalfa, roots of which have been reported to reach depths of 12 feet,
sugar beets with roots frequently more than 4 feet long, and bur oak
trees with roots that are known to penetrate 15 feet into the soil.
Plants with deep root systems are obviously more firmly anchored in
the soil than are those with shallow roots. Many other species of plants,
such as corn, blue grass and some other members of the grass family
have roots which are confined to the uppermost layers of the soil, chiefly
within 10 or 20 inches of the surface. Plants with shallow root systems
are best suited to grow in regions of scanty rainfall, which usually
reaches only the few upper inches of soil. Plants with deep root systems,
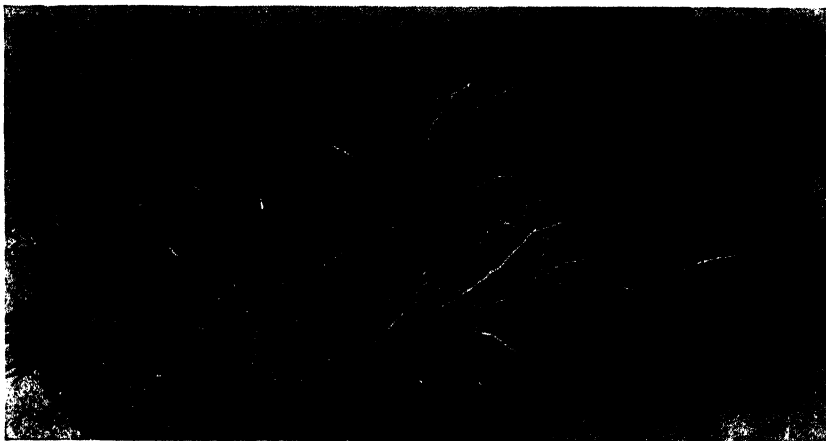
Fig. 19. Undersurface of a mat of blue-grass sod, showing fibrous roots and slender creeping stems (rhizomes). Sods are very effective soil binders.

Fig. 20. Exposed roots of white elm.
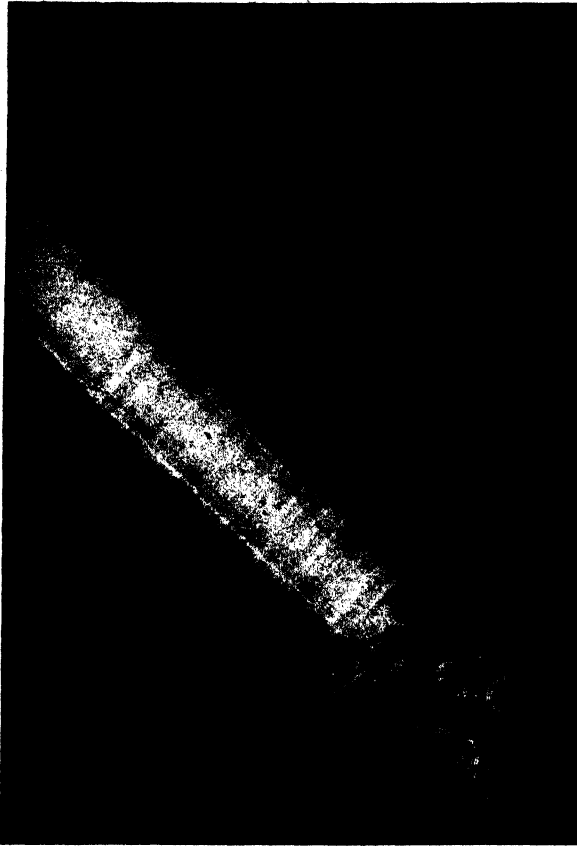
Fig. 21. *Pandanus* root
with root cap. 2x.
*Photo by Missouri Botanical
Garden*

on the contrary, can reach sources of water located deeper in the soil, water which is not ordinarily available to the shallower root systems. In some plants there are abundant roots in the surface layers of soil and likewise roots which penetrate deeply into the lower layers. Plants of this type, of course, have a great advantage over those species which have more restricted root systems. It is a difficult task to acquire complete information regarding the structure and extent of root systems because in digging up roots, or in removing the soil from them, many of the very small, fragile roots are torn away from the larger roots. Because of their location out of sight and because of the difficulty in removing entire root systems from the soil for study, the numbers of individual root branches and the total extent of these branches have. received little study. A recent publication on the root system of a rye

Photo by Missouri Botanical Garden
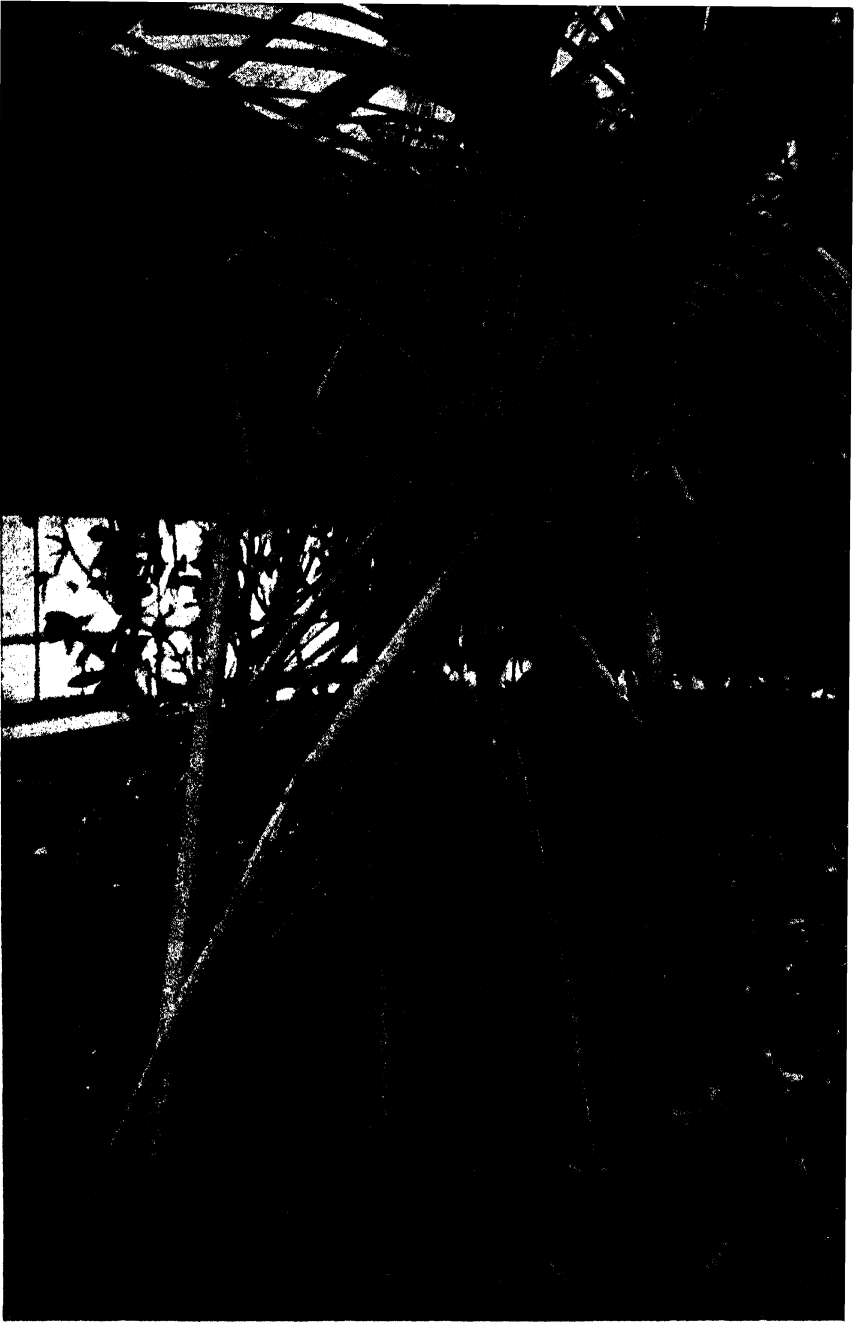
Fig. 22. Prop roots of *Pandanus*.

Fig. 23. Fruits and seedlings (at right) of mangrove. The seeds send out a tough, sharp-pointed root before they fall from the tree. When a seedling falls from a tree, the sharp root pierces the soil and anchors the seedling, which then continues its growth.

Photo by Missouri Botanical Garden

plant presents some astounding figures: total number of roots — 13,815,762, combined length of roots — 387 miles, total surface area of roots — 2,554 square feet. Contemplate the number of roots and their linear extent in a California Big Tree!

An examination of their external structure shows that roots are chiefly cylindrical in form. The tip of a root is usually bare of outgrowth for a length of one to several millimeters; above this bare tip are numerous **root hairs** (Figure 25), the principal absorptive structures of roots. These may be limited to a region a fraction of an inch long above the bare tip, or they may extend along the root for many inches, or even several feet. Root hairs are exceedingly fragile outgrowths of epidermal cells. They vary in length from sizes imperceptible to the naked eye to more than half an inch. Their especial significance lies in the fact that they increase enormously the absorbing surface of root systems. The above-mentioned investigation of the root system of a rye plant showed that there were over 14 billion root hairs on the plant, that the length of all these root hairs was about 6600 miles, and that the total surface area of all the roots and root hairs together was almost 7000 square feet. The minute structure of root hairs will be described in the next section of the chapter. The tip of a root is sometimes slightly

swollen. This swelling is the root cap, a thimble-shaped mass of cells which fits over the embryonic tissue situated just above the tip. Root caps are present in practically all roots, but in many cases they are too small to be visible to the naked eye. The root cap acts as a buffer which protects the fragile and important embryonic cells located above and partly within it.

4. THE MICROSCOPIC STRUCTURE OF ROOTS

If a longitudinally-cut, thin section of the terminal portion of a young root (Figure 24) is examined microscopically, four cell regions of rather different aspect are apparent. At the very tip is the **root cap** (Figure 21), already mentioned, a protective cover which fits over the **meristematic (embryonic) region,** in which cell division occurs very generally. The outer portion of the root cap is rather rough and uneven because the surface cells are worn away by contact with rock particles as the root tip pushes its way through the soil. The meristematic region just above the root cap produces new cells more or less continually, some of which are added to the inner portion of the root cap. Thus, the root cap is built up by new cells on its inner surface as the older cells of the outer surface are worn away. The cells of the **meristematic region** are small, thin-walled, and usually more or less cubical in form. They contain very dense protoplasm, in which the vacuoles are small and usually inconspicuous. When this region of the root is examined with the microscope, numerous cells with their nuclei in various stages of mitosis can be seen. This meristematic region, or root-growing point, is the cell-forming region which contributes largely to the growth of the root in length. Above the meristematic region is the **cell-elongation (cell-enlargement) region.** Here the cells newly formed as a result of mitosis and cell division in the embryonic region are undergoing rapid enlargement chiefly in the longitudinal direction. The cell walls increase in length and consequently the total volumes of the cells become larger. The protoplasm also increases in volume, but at a slower rate than the increase in the size of the cell cavity. The small vacuoles of the meristematic cells fuse usually into a single large, central vacuole in each cell of the elongation region. The large vacuole fills the major portion of the cell cavity with the protoplasm in the form of a thin layer outside the vacuole and pressed against the cell wall. The meristematic and elongation regions, together are seldom more than a millimeter or two in length. Above these regions is the **region of**
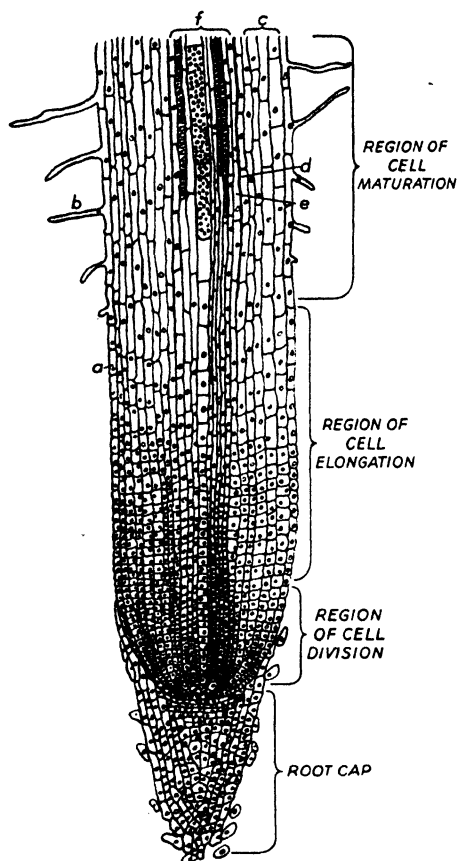
Fig. 24. Longitudinal section of a young root
of barley
a. epidermis.
b. root hair (a protuberance from an epidermal
cell).
c. cortex.
d. endodermis.
e. pericycle.
f. differentiating conducting tissues of stele.

maturation or **differentia-
tion.** Here the growing cells
of the elongation region are
undergoing division of labor
and an accompanying differ-
entiation of structure. Some
of them are transformed into
parenchyma cells, some into
xylem cells, others into
phloem cells and so on. All
of the portions of the root
above the elongation zone
may be termed the **matured
region,** for all of these por-
tions are composed of the
matured, differentiated tis-
sues of the root system.

In the younger part of the
maturation region are pro-
duced the root hairs. A root
hair is a slender, elongated
protuberance of a root epi-
dermal cell. Root hairs
should not be confused with
branch roots which often ap-
pear almost as small as hairs.
A branch root is a many-
celled structure with a root
cap, meristematic region,
xylem, phloem, etc., whereas
a root hair is an extended
portion of a single cell. A
root hair begins as a small
outgrowth of an epidermal
cell near the lower limits of the maturation zone (Figure 26). The rate
of growth of root hairs is usually fairly rapid and their life spans are
rather short, in most cases not more than a few days or rarely a few
weeks. Root hairs seldom reach lengths of more than a half inch. Shortly
after they reach their maximum size, they wither and die in the upper
portion of the **root hair zone,** the part of the maturation region from
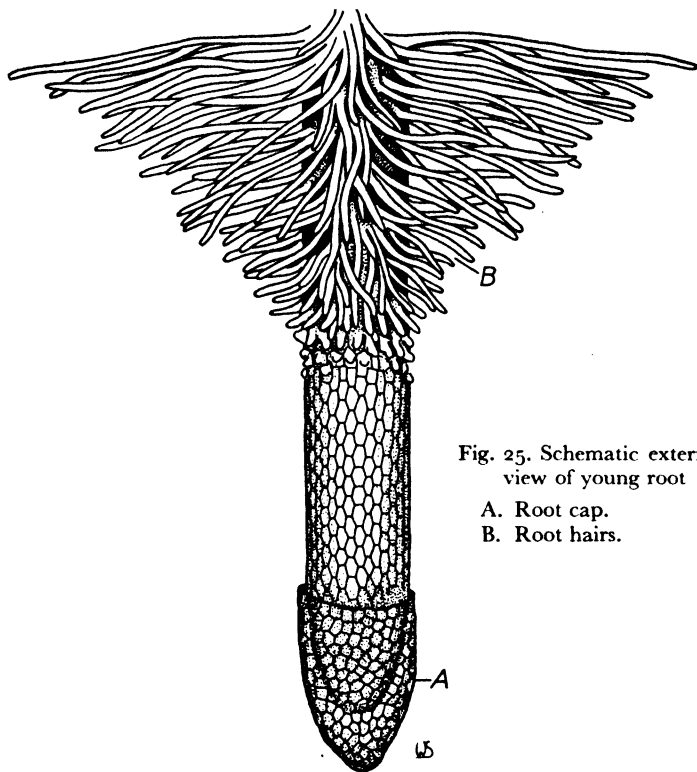
Fig. 25. Schematic external
view of young root

A. Root cap.
B. Root hairs.

which the root hairs grow. Root hairs grow in great profusion in this
zone; in some species of plants, there are more than 200 root hairs
growing from each square millimeter of root surface in the root hair
zone. This portion of the region of maturation is densely woolly in
appearance because of the numerous white root hairs (Figure 27). Data
on the sizes and numbers of root hairs are presented in the preceding
section. The production of new root hairs continues just above the re-
gion of elongation of the root tip as the tip grows downward into the
soil, the youngest root hairs developing always at about the same dis-
tance above the root tip. The oldest root hairs at the upper end of the
root hair zone may die off at about the same rate that the new root
hairs are produced at the lower end of the zone so that the total length
of the root covered with root hairs may remain fairly constant. As the
root tip grows farther into the soil, the root hairs develop immediately
behind it and thus are continually produced in new regions of the soil.
This is important to roots because their chief absorbing cells, the root

hairs, are thus brought in contact with new supplies of water and mineral salts.

Root hairs are very fragile and when they are exposed to dry air or bright, warm sunlight, they wither and die within a few minutes. If, in the transplantation of plants, soil is allowed to fall away from the roots, it usually carries with it most of the root hairs from that portion of the root system, for the root hairs are in intimate contact with the soil particles, twisting among and around them and often actually glued to them by viscous, colloidal materials in the root hair cell walls. Care should always be exercised in the moving of plants that the soil around the roots is taken with the plants, so that the delicate root hairs and small branch roots are carried along. The presence of such structures on plants in the process of being moved makes possible the continuous absorption of water during the moving and enables the plant to become established very quickly in its new location. If the root hairs are destroyed much absorptive surface of the root system is eliminated and the wilting and frequently the death of the plant follow. The chief significance of root hairs, of course, lies in the fact that they increase enormously the absorptive surface of the root system and that they continually reach new areas of the soil as the roots from which they grow penetrate the soil more deeply. Root hairs are present in most higher types of plants, with the exception of certain aquatic species.

The examination of a transverse or cross-section (Figure 28) of a root in the root hair zone of the maturation region shows several highly

Fig. 26. Epidermal cells of root showing development of root hairs

A. Vacuoles.   C. Nucleus.
B. Cytoplasm.   D. Cell walls.
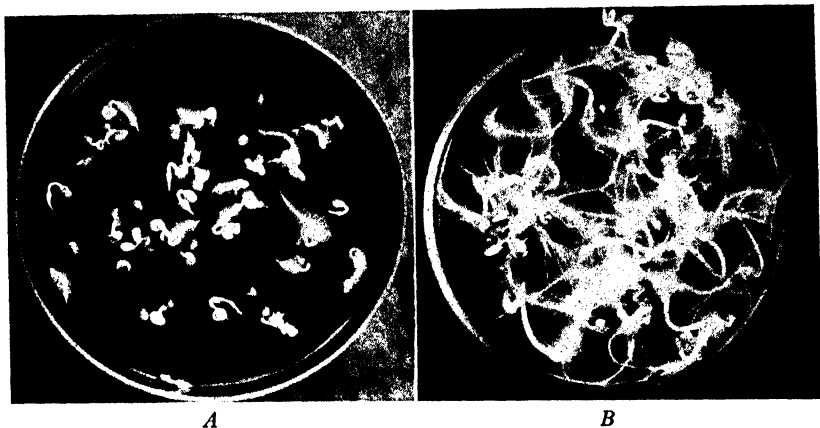
Fig. 27. Radish seedlings showing root hairs
A. Seedlings, 48 hours old.
B. Seedlings, 96 hours old.

differentiated tissues. The surface layer of cells, the **epidermis,** produces the root hairs and thus is an absorptive tissue, as well as a tissue which furnishes a certain amount of protection to the underlying cells. The **cortex** is inside of the epidermis and is composed of parenchyma cells which are rather large, thin-walled, and roughly spherical or ovoid in form. Numerous intercellular spaces occur in the cortex; these are important as avenues for the diffusion of water and of gases among the cortical cells. The cortex stores much of the reserve food which accumulates in the roots and also transports the water and salts absorbed by the root hairs to the conducting cells in the center of the root. Water moves inward from the root hair cells to the outermost cells of the cortex as a result of differences in the osmotic concentrations of the cell sap and water-absorbing cells. The movement of water from one cortical cell to another toward the conducting tissues likewise occurs as a result of differences in the osmotic concentrations of these cells. The inward diffusion of salts is also attributable in part to differences in the concentrations of those salts in the root hair and cortical cells. Inside the cortex is a single layer of cells called the **endodermis.** The cells of this layer are usually smaller and more nearly rectangular in appearance than the rounded cells of the cortex. The inner and radial (side) walls of the endodermal cells are usually conspicuously thickened, whereas the outer walls of these cells remain thin. A large part of this characteristic endodermal wall thickening is caused by the secre-
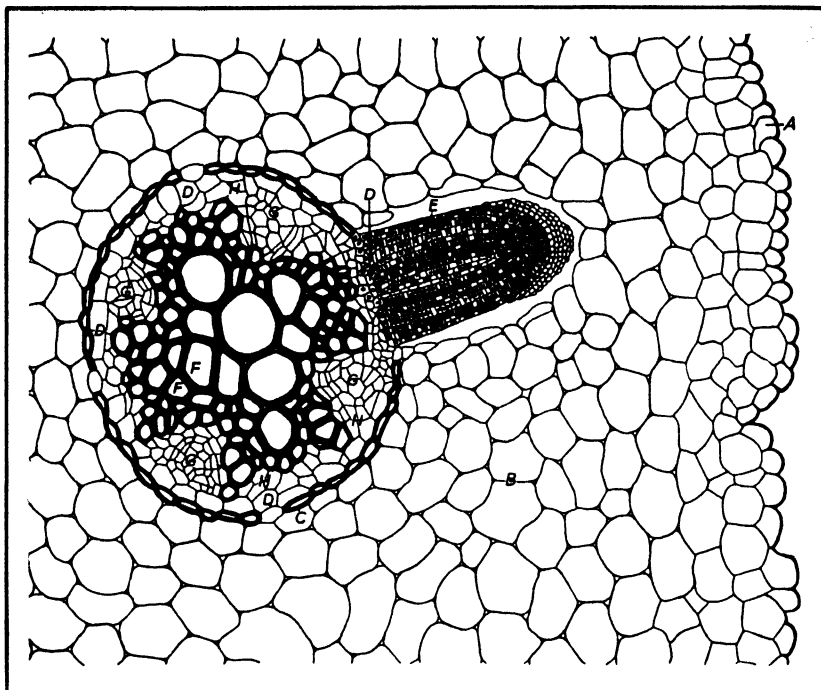
Fig. 28. Portion of root cross-section

A. Epidermis.   F. Xylem.
B. Cortex.   G. Phloem.
C. Endodermis.   H. Parenchyma of stele.
D. Pericycle.
E. Branch root originating from pericycle.

tion into the walls of **suberin,** a fatty material which is impermeable to water. The function of the endodermis is not known with certainty but it is believed that this layer of cells aids in the movement of water and minerals from cortex into the conducting cells of the xylem or acts as a water dam which prevents the outward escape into the cortex of water and other materials from the conducting cells inside the endodermis. The walls of the endodermal cells in the lower part of the root hair zone as a rule are not much thickened, so that water and solutes can easily pass inward through them and thus reach the conducting tissue. In older parts of the root, however, the endodermis is usually thickened and thus prevents the outward diffusion mentioned above, of materials which have passed into the conducting cells in younger parts of. the root. In the older endodermis, there are occasional thin-walled cells,

through which enough water and foods diffuse outward to nourish the cells of the cortex and epidermis.

The endodermis is the outer part of the **stele** or **vascular cylinder** (Figure 29), the strengthening and conducting portion of the root. The layer of cells just inside the endodermis is the **pericycle**, a layer of small, parenchyma cells, capable of producing new cells which grow outward from the stele and thus form branch roots. The origin of branch roots is thus internal with respect to the cortex and epidermis (Figure 30). Such root branches must force their way out through these latter tissues before they reach the soil. These branch roots are similar in structure, growth, and function, to the main roots from which they arise. Inside the pericycle is the **xylem** tissue, arranged usually in the form of a star, or in the form of separated groups of cells situated radially, like the spokes of a wheel. The xylem is composed of rather thick-walled conducting cells, chiefly vessels in most seed plants. These xylem cells also constitute the principal strengthening cells of roots. Xylem tissue conducts water and mineral salts upward into the stem and at certain times may also transport upward foods previously stored in root tissues. Located between adjacent points of the xylem star or situated in shorter bands alternating with the radially-arranged xylem groups are small clusters of **phloem** cells. These clusters are usually smaller than the xylem masses, and the cells of which they are composed are somewhat smaller and thinner-walled than those of the xylem. The phloem cells are chiefly sieve tubes and companion cells, both of which carry down into the root foods which have been manufactured in the leaves and transported down-ward through the phloem tissues of the stem. The alternate arrange-ment of xylem and phloem tissues in young roots is an advantageous one, for such arrangement makes possible ready access of these tissues to the root cortex through which water and minerals move into the stele and in which water and foods are commonly stored. In most kinds of plants the xylem "star" constitutes the entire middle portion of the stele. In a smaller number of species, however, the center of the stele is made up of a mass of parenchyma cells, with the groups of xylem cells situated outside of the parenchymatous core (Figure 31).

The tissues thus far described in roots are **primary tissues,** that is, they develop from a terminal growing point, namely, the meristematic region of the young root; primary tissues are involved chiefly in growth in length. The roots of most trees, shrubs, and other types of perennial plants have **secondary tissues** in addition to the above mentioned primary tissues. Secondary tissues are those produced by a **cambium;**
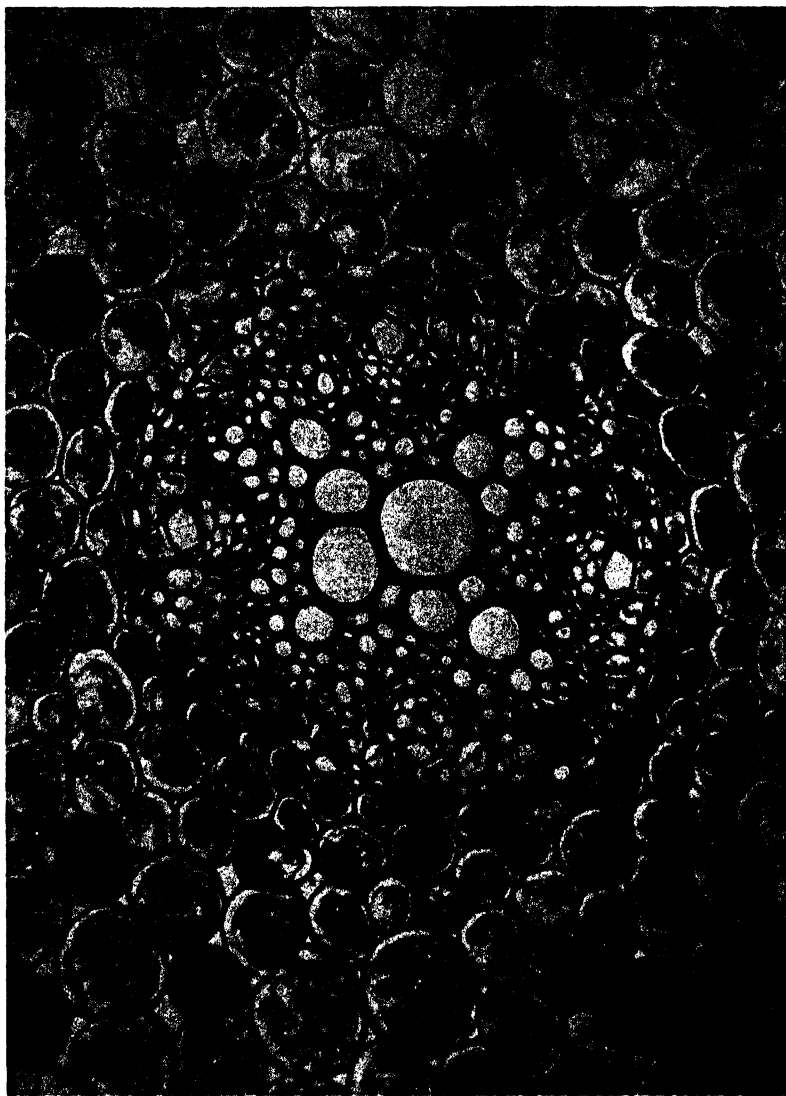
Fig. 29. Photomicrograph of cross-section of buttercup root (see Figure 28 for labels; note starch grains in cortex cells).
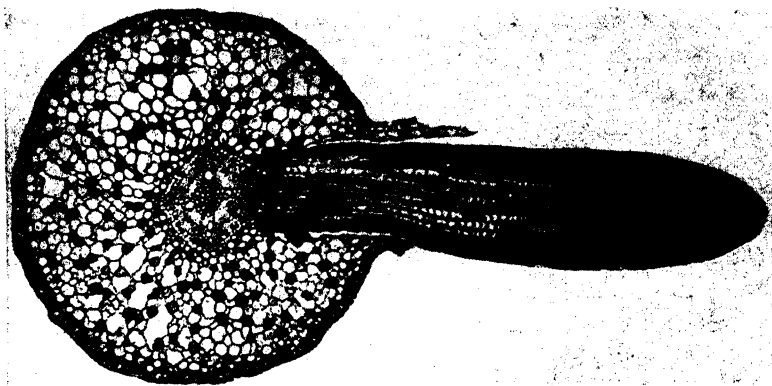
Fig. 30. Photomicrograph of a root cross-section, showing the origin of a branch root from the pericycle.

they are formed in a transverse direction in stems and roots, as contrasted with primary tissues which are formed chiefly in a longitudinal direction. Thus, secondary tissues are involved chiefly in increase in diameter of roots and stems. In perennial roots of many plants, a cambium layer, termed the **cork cambium,** frequently develops in the pericycle tissue. The cells produced by the cork cambium on its outer surface become suberized and thus waterproofed and are termed **cork cells.** The epidermis and cortex disintegrate as cork cells develop, and their protective function is taken over by these cork cells. The older roots of perennials are thus frequently covered with a corky layer much like that of the outer bark of the stem. In many plants, roots never become thickened beyond the extent of their primary tissues (e.g., in most annual plants), but in perennials roots usually grow considerably in diameter as a result of the formation of secondary tissues. These tissues are produced by the growth activity of a true **cambium** layer which develops from certain parenchyma cells lying between the xylem and phloem groups and from some of the pericycle cells. The cambium develops in such a way that the xylem cells are inside it and the phloem cells outside. The cambium layer, which is only one cell thick, forms by cell division new xylem cells inside itself and new phloem cells outside itself. These are added to their respective primary tissues, and their continued formation brings about the greater part of the transverse growth of the roots of woody plants. The cambium forms xylem cells more rapidly than it does phloem cells, so that ultimately the xylem, or wood, constitutes the greater part of the total volume of
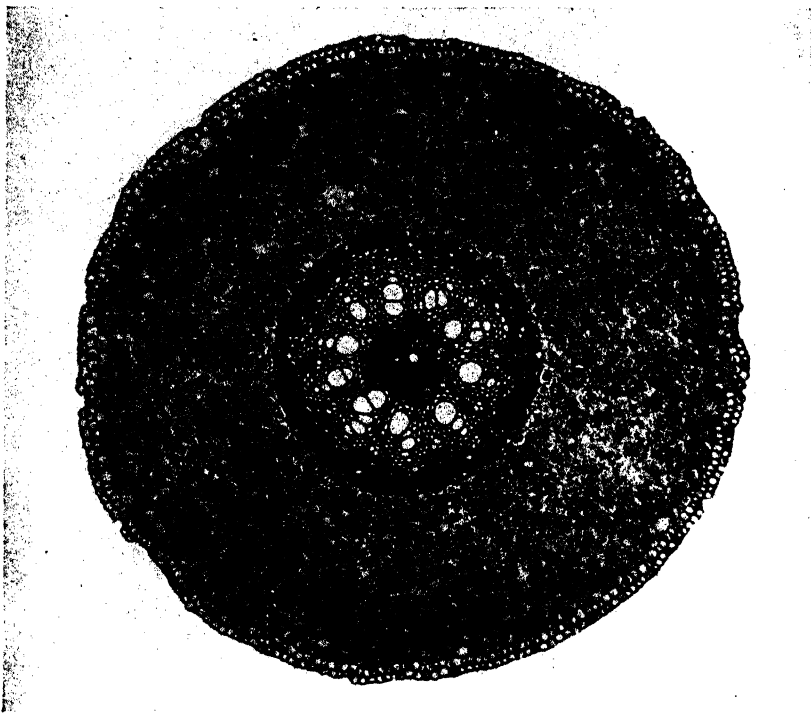
Photo by Triarch Botanical Products

Fig. 31. Photomicrograph of a cross-section of a monocotyledonous root (*Smilax*), showing an epidermis on the surface, a well-developed cortex, an endodermis, with dark, thickened walls, ten groups of large-celled xylem, and alternating with them the smaller groups of small phloem cells. The cells surrounding the xylem and phloem tissues are parenchyma cells.

such roots. Older roots with secondary tissues are much like woody stems in structure, with a surface layer of *bark*, a large woody cylinder inside the bark, and a cambium layer between the two.

5. THE ABSORPTION OF MATERIALS FROM SOILS BY ROOTS

As described in the preceding chapter, the absorption by living cells of water and substances dissolved in water involves several complex forces which are only imperfectly known by plant physiologists. Both osmosis and imbibition are operative in the absorption of ·water from the soil by the surface cells of roots and in the transfer of water

from cell to cell across the cortex of the root to the stele. The intake of solutes from the soil and their passage through the cortex to the stele are accomplished in part as a result of simple diffusion, in part by active physiological absorption of solute particles (molecules and ions) against a concentration gradient of such particles.

In addition to these generalizations concerning water and solute absorption by root cells, several other conclusions can be drawn from numerous investigations of absorption phenomena. Among these are the facts that solutes may be absorbed by root hair cells independently of the direction of movement of water, that the entrance of any particular solute into root hairs is in the main independent of the entrance of other kinds of solutes, and that both water and solutes, as they are absorbed by root hairs, do not remain in these cells but move into other cells of roots and ultimately into the conducting cells of the stele which carry them upward into stem and leaf cells.

An important and as yet unsolved question concerning the absorption of water by roots is whether osmotic or imbibitional forces are the more important in bringing water into the absorbing cells of roots. Ordinarily the osmotic concentration of the cell sap of root epidermal cells is higher than that of the soil solution and this superiority seems to be maintained when the concentration of the soil solution is increased. This would seem to constitute a mechanism which ensures continued absorption of water by osmotic action, since, as has been pointed out in an earlier chapter, water usually diffuses from a region of low osmotic concentration of solutes (or high concentration of water) toward a region of high osmotic concentration of solutes (or low concentration of water).

However, studies of the rate of evaporation (**transpiration**) from the aerial parts of plants indicate that absorption by osmosis is apparently too slow to replace the water lost by such evaporation. Many physiologists believe that under conditions of moderate to rapid transpiration, the movement of water from the soil into root cells is principally by imbibition; according to this theory, the evaporation of water from leaf cells causes these cells to absorb water largely by imbibition from the water-conducting tissues of leaves and that these tissues in turn, as they give up water to the drying leaf cells, take up water rapidly from the conducting tissues of stems which are continuous with those of roots; the conducting tissues of roots then take water from the cortical cells of roots, which then imbibe water from the root epidermal cells. These epidermal cells in their turn take in water

chiefly by imbibition from the soil solution. According to this idea, the action of the absorbing cells of roots in taking up water is chiefly passive, the imbibitional forces being more important than osmotic forces and the root acting largely as a filter in water intake.   Evidence in support of this theory is derived in part from experiments which have shown that dead root systems can continue to absorb water for several days after they have been killed, provided that evaporation from the aerial parts of the plants is rather rapid; in dead root systems, osmotic forces are non-existent, for such forces in plants depend upon the existence of living protoplasm in the absorbing tissues. It should be pointed out in this experiment that the dead roots do not continue to absorb water *indefinitely;* that is, for normal, continued absorption of water by roots, *living cells must be present.* Under conditions of low transpiration it is likely that living roots absorb water principally by osmotic forces. Though precise information concerning the relative effectiveness of osmotic and imbibitional forces in water absorption by roots is lacking, it is certain that both types of forces are important and that their relative importance varies with a number of conditions, such as transpiration rates, concentration of the soil solution, etc.

The movement of water from the living cells of the cortex through the endodermis into the non-living xylem cells of the root stele is the least understood of all the phenomena involved in water movement in plants. Various theories have been proposed to explain the passage of water into xylem cells but no one of them is supported by sufficient experimental evidence to warrant its acceptance as a satisfactory explanation. Under conditions of low transpiration (e.g., in the spring before the growth of leaves) and rather rapid water absorption, the cells of the cortex and endodermis seem to force water under pressure into conducting cells of the xylem. This pressure, known as **root pressure,** is apparent if one severs a stem from a root; water and dissolved substances are exuded from the cut stump, a phenomenon termed "bleeding." This bleeding may continue for days in certain plants, for example, from the stumps of pruned grape vines. The actual forces involved in the transmission of water by way of the endodermis into the conducting cells of the root xylem have not been satisfactorily explained, however. Under conditions of rapid transpiration, root pressure is not apparent and still water moves from the root cortex through the endodermis into the root xylem, probably as a result of the imbibitional pull of transpiring leaf cells.

When the water and dissolved materials have entered the xylem

cells, their upward movement is a result of forces other than osmotic forces, for the xylem cells are non-living and since they lack protoplasm and membranes are unable to function osmotically. The movement of such materials upward through the non-living tracheids and vessels of the xylem is a mass movement, in which the water and solutes are carried upward apparently by forces developed as a result of transpiration from leaf cells, as will be described in the chapter on stem physiology.

6. SPECIALIZED ROOTS

In some species of plants, specialized or modified roots perform functions other than the usual root functions of anchorage, absorption, conduction, and food storage. In some plants, roots perform **reproductive** functions. The roots of cherry, apple, and other species of trees produce "suckers" which develop into new plants, and sweet potatoes and dahlias are commonly propagated by man by means of roots. Some plants, such as corn, screwpine, and banyan trees produce adventitious prop roots which arise from aerial portions of the stem and grow downward until they reach the soil. The chief function of such roots is to give added support to the stem system. The mangrove trees of tropical seashores send down prop roots which reach the water and grow into the sand below the water. The numerous prop roots of these plants become entangled into dense masses which collect drifting leaves, sticks, and sand, and thus build up soil. In some plants, adventitious roots act as climbing roots, which anchor stems to the walls, fences, and trees along which they grow. Roots of this type are found in poison ivy, English ivy, and other species of vines. The spongy **aerial** roots of **epiphytic** orchids (epiphytes are plants which gain physical support from telephone poles, trees, roofs of houses, etc.) take water from falling rain and atmospheric humidity, absorb raw materials from the debris which collects about them and help to anchor the whole plant to the object upon which it grows. Sometimes these aerial roots are green, as in the vanilla plant, which is an orchid, and are thus able to manufacture food. Bald cypress trees in swamps develop peculiar root projections which grow upward above the surface of the water or swamp soil in which the trees grow. These are called "knees" (pneumatophores) whose function seems to be to transmit air downward into the tissues of the submerged roots. Certain parasitic seed plants, such as **dodders** and mistletoe, absorb their food directly from other plants,

Photo by C. F. Hottes
Fig. 32. Pneumatophores of bald cypress.

and do not have contact with the soil during most of their lives. Their roots are modified into suckers (**haustoria**) which penetrate the tissues of their **host plants** and absorb food directly from them. Certain types of bulbs and other kinds of underground stems have contractile roots which actually pull the stems, from which they grow, more deeply into the soil. Enormously enlarged storage roots, such as those of rutabagas and turnips, might be considered as specialized roots, but in addition to the storage of large amounts of food, they perform the other typical functions of roots — absorption, anchorage, and conduction. Thus they are not specialized to the same degree as the other roots described in this section.

7. ECONOMIC SIGNIFICANCE OF ROOTS

The fundamental importance of roots in the scheme of nature and in man's existence needs no further discussion, except to reiterate that the growth of all higher plants, upon which man depends, would be

impossible without roots. It is of interest to mention some specific plants, the roots of which are directly useful to man. Among these are a number of medicinal plants: aconite, asafetida, gentian, goldenseal, ginseng, licorice, rhubarb, marshmallow, and valerian, all of which are important in pharmaceutical preparations. The principal root crops used as food by man are: beets, carrots, salsify, parsnips, radishes, turnips, rutabagas, sweet potatoes, yams, and cassava (tapioca). Spices and other aromatic substances are furnished by the roots of several species of plants: angelica, horseradish, sarsaparilla, turmeric, and sassafras. The roots of madder and alkanna furnish important dyes, the former being the source of the widely used "turkey-red."

In addition to these uses, the importance of roots as soil-binders and preventers of erosion should be emphasized once more.

SUMMARY

1. The chief functions of roots are:

a. The absorption of water and dissolved mineral salts from the soil.

b. The firm anchorage of plants in the soil.

c. The conduction of absorbed materials up into stems and the transfer of foods manufactured in leaves downward through the roots.

d. The storage of food.

2. The roots of plants normally grow in soils.

3. Soils are composed of air, water, rock particles, soluble inorganic chemical compounds, organic matter, and living organisms.

4. Soils vary greatly in the relative proportions of these substances present in them.

5. Most plants grow best in well-aerated soils, for oxygen is required for normal respiration in roots.

6. Water which drains away through soils or runs off them rapidly is largely unavailable to plants. The water which is loosely held among the soil particles furnishes the greater part of the available supply of water for plant roots.

7. There is considerable movement of water in soils, laterally as well as vertically. Capillary forces in the soil are in large part responsible for such movement.

8. Rock particles vary greatly in size in soils. Certain kinds of rock particles are disintegrated by carbonic acid, formed by the excretion of CO_2 by roots.

9. The soluble inorganic salts in soils furnish the minerals necessary for normal plant growth.

10. Organic matter develops in soils from the decomposition of the waste products and dead remains of plants and animals. Organic matter influences the physical properties of soils and in its disintegration restores minerals to the soil, thus aiding in the maintenance of soil fertility.

11. Many of the substances present in soils occur in colloidal condition.

12. Bacteria, higher fungi, insects, worms, and rodents are the principal organisms present in soils. These organisms increase the organic matter in soils and also influence the physical qualities of soils.

13. Plants influence soils in these ways:

a. They absorb substances, chiefly water and minerals, from soils, and excrete CO_2, which aids in the decomposition of rock particles.

b. The decomposition of dead plant-parts adds organic matter to soils.

c. Their roots tend to hold the soil and prevent its erosion by wind and water.

14. A primary root develops from the radicle of a seed. The branches of primary roots are secondary roots. Roots which arise from some structure other than a primary root or its branches are called adventitious.

15. The entire mass of roots of a plant is called its root system. There are two principal types of root systems: tap and diffuse (fibrous).

16. Root systems vary greatly in their degree of branching, depth of penetration, rate of growth, etc.

17. Roots are typically cylindrical in form.

18. The tip of a root is covered by a protective root cap.

19. Immediately above the root cap is the meristematic region (region of cell division) in which new cells are formed. Above this is the region of cell elongation in which the newly formed cells undergo enlargement, chiefly in length. Above the region of elongation is the region of cell maturation in which the mature tissues of the root undergo differentiation. Root hairs cover part of the region of maturation.

20. A root hair is a protuberance from a root epidermal cell.

21. Root hairs increase the absorptive surfaces of roots.

22. Root hairs are very fragile and usually short-lived and are easily destroyed. They make intimate contacts with soil particles.

23. In cross-section the maturation region of a young root shows the following tissues, from outside in:

a. Epidermis.

b. Cortex.

c. Stele, consisting of endodermis, pericycle, xylem, phloem, and parenchyma tissue. The primary xylem and phloem tissues are radially arranged.

24. Older roots may develop a cambium tissue from parenchyma cells between the xylem and phloem tissues. The cambium forms secondary xylem and phloem cells and is in large part responsible for the growth of roots in diameter.

25. Old roots are covered by cork tissue, as are most woody stems.

26. Root hairs (and other epidermal cells of roots) absorb water by imbibition and osmosis, and solutes chiefly by active absorption. The same forces are in large part responsible for the movement of water and solutes across the cortex and endodermis into the stele.

27. The evaporation of water from leaves develops forces which are transmitted through water columns in the xylem and which accelerate the movement of water and solutes through the living cells of roots into the stele.

28. Water and solutes move upward chiefly through the xylem cells of roots.

29. Examples of morphologically specialized roots with rather specialized functions are:

a. Prop roots of corn, pandanus, etc.

b. Climbing roots of English ivy.

c. Spongy, aerial, water-absorbing roots of epiphytes.

d. Knees (pneumatophores) of bald cypress.

e. Suckers (haustoria) of dodders and mistletoe.

f. Contractile roots of bulbs.

The Gross Structure of Stems

1. THE ORIGIN AND NATURE OF STEMS

THE FIRST stem of a seed plant has its origin from a portion of the embryo axis in the seed known as the **epicotyl**, which is a continuation of the **hypocotyl**, the structure from the tip (radicle) of which the primary root develops. The epicotyl is a cylindrical structure with a small bit of meristematic tissue and frequently a pair of tiny leaves at its apex. When a seed germinates, the radicle is usually first to emerge. This behavior is important, for since the radicle (root primordium) develops into the first root of the seedling, its early entrance into the soil makes it possible for the embryo to begin absorbing the water and minerals necessary for its future development before the reserves of the seed are exhausted. Soon after the emergence of the radicle, the epicotyl leaves the seed coat and begins its upward growth through the soil toward the light and air. In some cases, the hypocotyl remains below the surface of the ground, and the entire stem develops from the epicotyl, as in the garden pea plant. In other plants, the garden bean, for example, the upper portion of the hypocotyl rises above the surface of the soil for several inches; in this case, the basal portion of the stem is developed from the hypocotyl, the remainder from the epicotyl.

There are two chief functions of stems: the conduction of materials and the production and support of leaves and reproductive structures. Other functions of the stems of certain plants to be described in greater detail later are food storage, food manufacture, reproduction, etc.

A stem with its leaves is called a **shoot**, an entire stem with all of its branches and leaves, a **shoot system**. Stems which grow above the soil are termed **aerial stems** to distinguish them from the underground, or **subterranean stems**. The stems of seed plants are chiefly aerial. The aerial stems of most plants are **erect**, as in elm trees, petunias, and corn, but in some species, such as morning-glories and grapes, the stems have a **climbing** habit of growth. In still other species, such as straw-
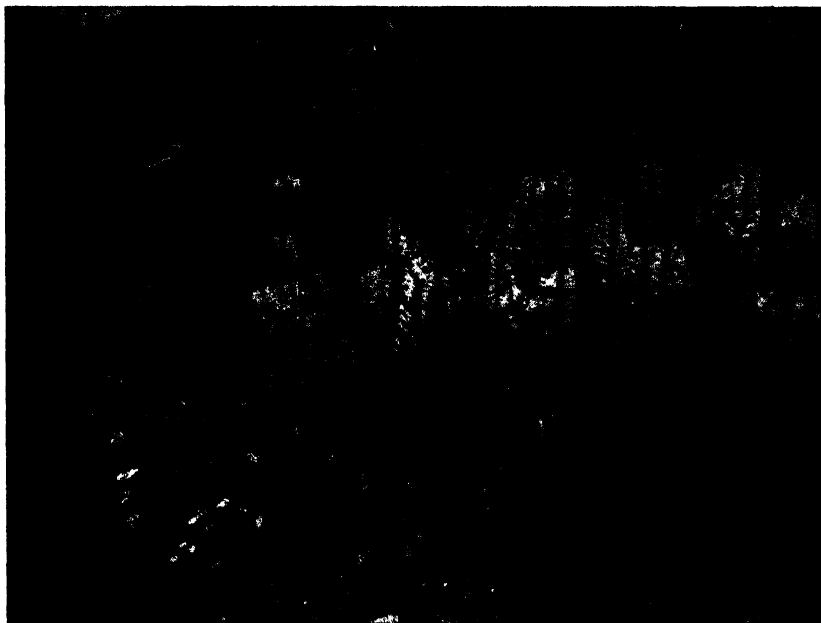
Fig. 33. False dragon's head (*Physostegia virginiana*), with herbaceous stems.

berries, watermelon, and cucumbers, the aerial stems are **prostrate** or creeping — that is, they are not strong enough to become erect, but grow in a horizontal direction over the surface of the soil. Subterranean stems likewise show a variety of growth habits which will be described later in this chapter.

2. THE EXTERNAL STRUCTURE OF STEMS

Stems vary a great deal in different species of plants in their external form, size, internal structure, longevity, and in other aspects. From the standpoint of their structural features and their growth habits, aerial stems may be divided into types: **herbaceous** and **woody**. Herbaceous stems are (Figure 33) rather soft and green, with virtually no development of tough, woody tissue, and with relatively little growth in diameter. The tissues of herbaceous stems are largely, sometimes entirely, primary tissue. Herbaceous stems are covered with an epidermis, and as a rule are annual — that is, their life-span is only one growing season. Some plants may have annual stems, with perennial roots, in

Photo by Missouri Botanical Garden

Fig. 34. Maidenhair tree, *Ginkgo biloba.*

which case the stems are usually herbaceous, the roots often woody. In certain types of hibiscus, this situation obtains. Likewise, in larkspur, columbines, and hollyhocks, the stems are chiefly annual but the roots are perennial. In such plants as peas and squash, both roots and stems are annual and the plants thus live only one season, not for a number of years as in the case of hollyhocks and columbines. Some annual stems, such as those of sunflowers, develop moderate amounts of wood, but annual stems in most cases are distinctly herbaceous. Most woody stems are perennial, remaining alive and active for more than two years. Stems of this type are composed chiefly of secondary tissues, most of which are xylem or wood. Woody stems are thicker, harder, and tougher than herbaceous stems, and since their surfaces are covered with cork cells, which replace the epidermis of very young twigs, they are usually rough in surface texture and lack the green color of herbaceous stems. Also, since they grow for a number of years, woody stems are usually much taller, as well as thicker, than herbaceous stems. A **tree** is a woody-stemmed plant which possesses a main stem, or **trunk**, which rises some distance above the ground before it branches (Figure 34). A **shrub** is a woody plant in which usually several stems of approximately equal size appear above the soil line (Figure 35). The maximum size attained by shrubs is less than that reached by most trees.

Occasionally there are difficulties in attempting sharp distinctions among the various types of stems described in the preceding paragraph. Sunflowers, already mentioned, have stems which are green, lack corky
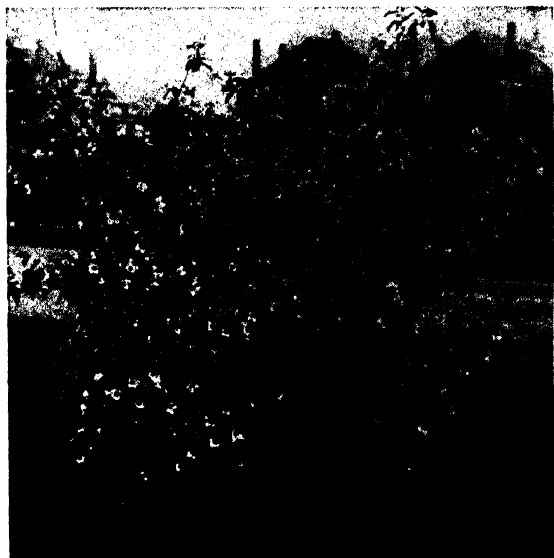
Fig. 35. *Philadelphus,*
a shrub.
*Photo by Missouri Botanical
Garden*

bark, and live for a single year, but which possess a moderate amount
of woody tissue. Stems which are herbaceous annuals in one region
may become perennial woody plants in another — the stems of tomato
plants and castor beans, for example, behave as annuals in the cooler
portions of the temperate zones, and as perennials in the tropics. Fur-
ther, the distinction between trees and shrubs is difficult in some species
of plants.

An examination of the surface of a stem in active, growing condition
shows a variety of structures, most common of which are **buds** and
leaves. Leaves are usually broad and flattened, or needle-like, ap-
pendages of stems. The point on a stem from which a leaf develops is
called a **node,** the section of stem between two successive nodes, an
internode. A node is thus not an actual structure, but is a position, or
location. Internodes are sometimes very short, as on the spur twigs
of an apple, or in other species, such as willows and sunflowers they
may be several inches long. In the upper angle between the point of
juncture of a leaf stalk with a stem is located, as a rule, a **bud.** This
angle between the leaf stalk and the stem is termed the **leaf axil,** and
the buds found in leaf axils are accordingly called **axillary,** or since
they occur along the sides of a stem, **lateral buds.** At the tip of each
stem or twig is usually located a **terminal bud.** Terminal buds and
axillary buds are usually similar in structure and in function; the dis-
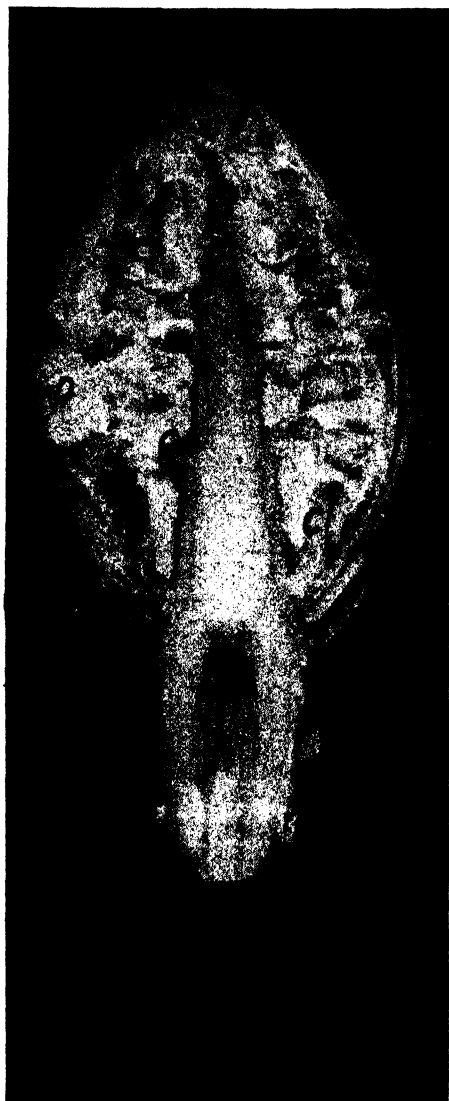
Fig. 36. Longitudinal section of
horse-chestnut bud

A. Bud scales.
B. Growing point of bud.
C. Rudimentary leaves.
D. Protective hairs.

tinction between them is chiefly one of position in most species of plants. Occasionally buds arise at places other than in the axils of leaves. Buds of this type are called **adventitious** (Figures 43, 44). They sometimes develop as a result of injury; for example, they are frequently found producing young shoots on the stumps of trees which have been felled. Structurally, they are like the normal type of buds which occur in leaf axils.

A bud (Figure 36) is essentially a convex, or cone-shaped mass of meristematic tissue, which produces laterally small projections, the rudiments of leaves, which develop, as the bud grows, into the mature leaves of the plant. Thus, a bud, since it contains the primordia of leaves, possesses nodes and also very short internodes, and is consequently to be regarded as a very much shortened, compact, undeveloped section of a stem. In **naked** buds, the meristematic tissue is exposed to the air without any protective covering other than embryonic leaves (Figure 37); buds of this type are found in most herbaceous plants (Figure 38) and in certain woody species in very moist regions of the tropics. In woody stems of the
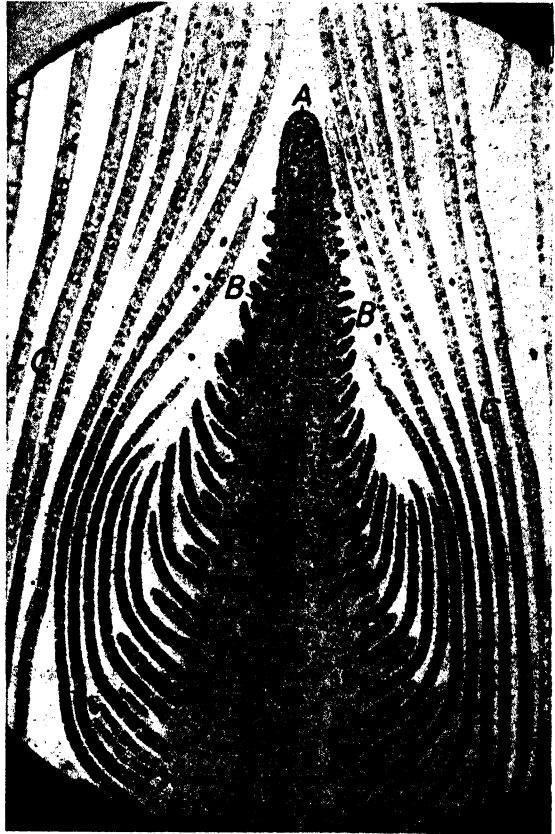
Fig. 37. Longitudinal section of naked bud and portion of stem of *Elodea*, a water plant

A. Growing point.
B. Leaf primordia.
C. Mature leaves.
D. Axillary buds.

dryer portions of the tropics and generally in the temperate zones, buds are **covered** with overlapping scales, known as **bud-scales**. These are modified leaves which grow out from the base of a bud and which form a protective coat over the meristematic tissue. These scales are often thick and tough and frequently, as in cottonwoods, are covered with a gummy secretion, or, as in some willows, with a dense growth of hairs. These scales protect the meristematic tissue from desiccation, and to a certain extent from mechanical injury, excessively low temperature, and the entry of various kinds of parasites.

Buds may be classified also on the basis of their activity, their arrangement on the stem, and the kinds of structures which they produce. Those buds which grow are called **active** buds to distinguish them from the occasional buds which remain inactive; the latter are called **inactive** buds and are usually axillary in position and situated at some
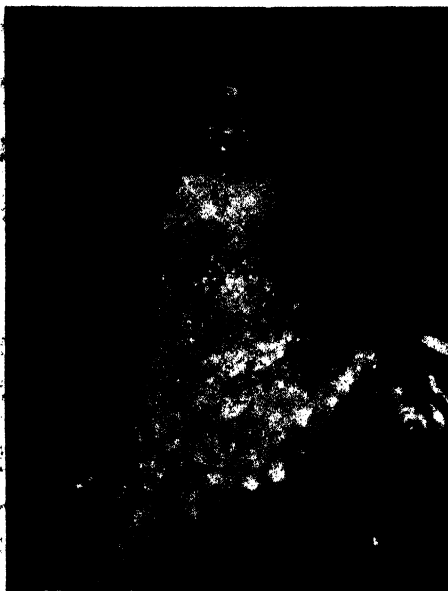
Fig. 38. Growing point of young oat stem, enveloped by two young leaves.

distance below the terminal bud of the twig upon which they occur. Sometimes these inactive buds develop many years after they are formed; they remain imbedded in the bark as the stem grows in diameter and under an appropriate stimulus may grow out into branches. Such behavior as this, of course, occurs only in perennial, woody stems. More frequently, however, inactive buds remain undeveloped during their entire existence. Buds differ, likewise, in their arrangement. In most plants, as in elms or apples, they are arranged in **alternate** or **spiral** fashion; that is, one bud occurs at each node and the successive buds from the base toward the apex of a stem may be connected by a continuous spiral line. In a lesser, though still rather large number of species, including maples, dogwood, and buckeye, the buds are arranged in **opposite** (Figure 39) manner; that is, there are two buds at a node on opposite sides of the stem. The **whorled** arrangement is uncommon, occurring in relatively few plants, such as catalpa, in the stems of which there are three buds at a node, more or less equally spaced about the stem. In some members of the coffee family, there may be six or more buds in whorled fashion at a node. Buds differ also in the nature of the structures which are produced by them. Thus, there are **flower buds,** which produce only flowers, as in roses and morning-glories, **stem buds,** sometimes called also **branch buds,** which grow out into new lengths of twigs, bearing leaves, and which occur in virtually all species of seed plants, and **mixed buds,** such as the buds of buckeye and apple, which produce both leaf-bearing twigs and flowers.

A longitudinal section of a stem bud, the most common kind of bud in seed plants, shows the convex meristematic region with the rudimentary leaves appearing in succession below the meristematic tip

(growing point) of the bud, with largest and oldest leaf primordia at the base of the bud and with progressively smaller leaf rudiments toward the growing point. These leaf primordia are arranged in spiral, opposite, or whorled manner, just as the leaves are in mature twigs, each with a tiny bud-rudiment in its axil. Thus a bud possesses minute leaves, and in their axils, buds, and of course nodes and internodes. The axillary bud primordia are not apparent in all species before the opening of the bud, however. The increase in length of a stem is caused largely by the rapid increase in length of the tiny internodes of the terminal bud as the bud develops. In most annual plants and in many woody plants of the tropics, the elongation of the internodes produced by the bud continues through most of the growing season, but in woody plants of
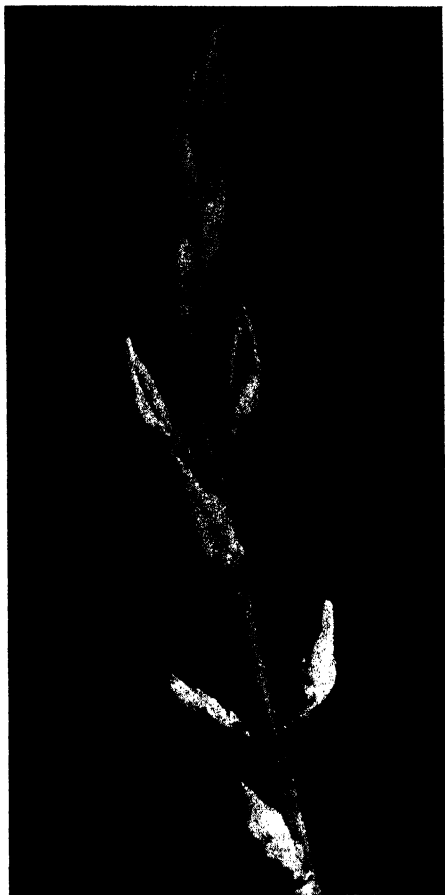
Fig. 39. Opposite buds of *Euonymus alatus*.

cooler regions, the elongation of these internodes occurs chiefly during a few weeks of spring, immediately following the opening of the bud scales. When a leaf bud "opens" its internodes elongate and the leaf primordia enlarge into the mature leaves of the twig. The first terminal bud of a stem develops from the apex of the epicotyl and as it grows, additional buds are formed in the axils of the leaf primordia of this terminal bud. At the end of the growing season of annual plants, with the death of the plant, the activity of its buds, which are naked, is at an end. In woody plants, the buds of which are usually covered, when a bud opens, the bud scales begin to grow more rapidly on their inner surfaces than on their outer, and, as a result, bend away from
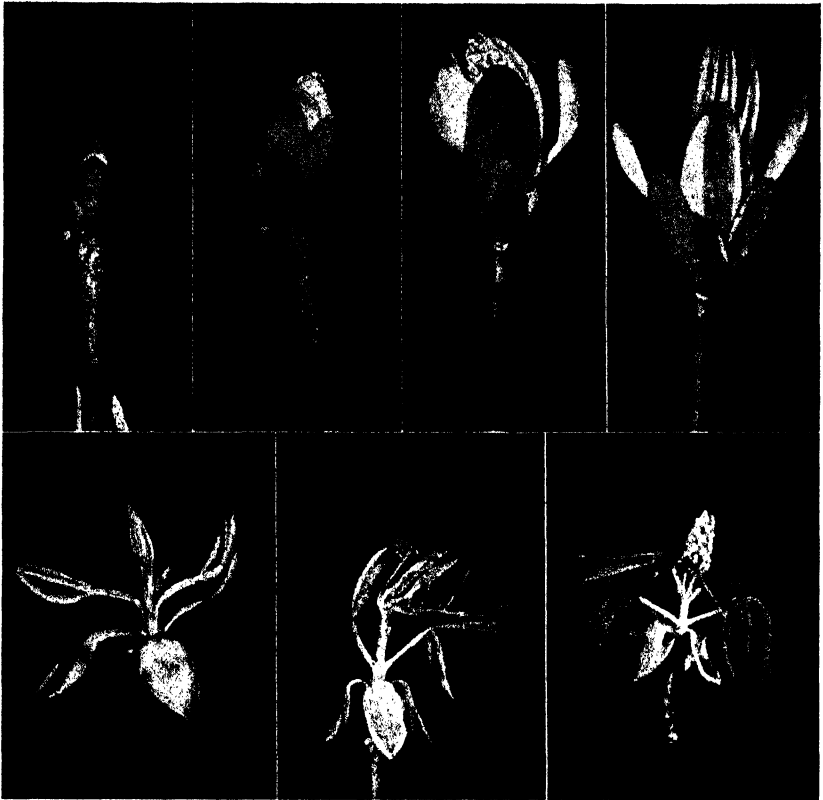
Fig. 40. Stages in the opening of the terminal mixed bud of a buckeye twig.

the center of the bud. With the separation of the bud scales, the elonga-
tion of the internodes of the bud and the enlargement of the leaf
primordia begin, and a new section of twig is formed (Figure 40).
The bud scales usually fall away a short time after they have opened.
During the growth season of the new section of twig, the bud primordia
which form in the leaf axils begin to enlarge so that at the end of this
growing season, a new terminal bud, similar in structure to that from
which the new section of twig grew, is present at the tip of this stem
section, with new axillary buds in all the leaf axils. These buds remain
quiescent during the remainder of the summer and throughout the
following winter, and with the coming of the next spring they begin to
grow in the fashion described above. The buds of woody plants 'are
often called **winter buds**, since they live through the winter. The

growth of a terminal bud produces elongation of a stem, that of an axillary bud produces a branch or twig of such a stem. When an axillary bud forms a branch twig, this twig develops its own terminal and axillary buds so that it has the same type of bud equipment as the main stem of which it is a branch. The axillary buds of this branch may grow subsequently and form a further order of branches of the branch twig. Thus, terminal buds produce growth in length of a twig, axillary buds produce branches of that twig. The origin of stem branches, then, may be described as **external** since the axillary buds which produce these branches are located on the surface of the stem. In many plants, the branches formed by the growth of certain axillary buds are **flowers** or **cones,** which are highly specialized twigs. In such cases the growth of this specialized, reproductive branch ceases; no buds are formed as a rule in the axils of the floral organs and thus no further growth of such a twig is possible. After fulfilling its reproductive function, the flower or cone usually withers and falls away from the main twig of which it is a branch. In annual plants the terminal bud of the stem is often transformed into a flower, following which the growth in length of stem ceases.

In some species of plants, for example, lilacs, the terminal bud of a twig fails to develop. In such a case, the axillary buds nearest the terminal bud grow into new sections of the stem, taking over, as it were, the function of the terminal bud. In other species, such as buckeye and hickory, the terminal bud is the most active one and its growth is responsible for the increase in length of the twig at the apex of which it is situated. The positions, sizes, forms, and surface nature of buds are so characteristic of different species of plants that they are commonly used for identification, particularly during the winter when leaves and flowers are not present.

The form of a whole shoot system is determined in a large degree by the positions, arrangements, and relative activities of the various types of buds. If the axillary buds are opposite, the branches produced by them are opposite, if they are alternate, the branches into which they grow are alternate. If there is a dominant terminal bud with a relatively large number of dormant axillary buds, the branch on which these buds occur will be much elongated with relatively few side branches. If, on the contrary, the terminal bud is slow-growing and the axillary buds are active, the stem will grow slowly in length and will possess many, relatively fast-growing branches. By applying his knowledge of bud behavior, a horticulturist can control the shape of plants

Fig. 42. Portion of horse-chestnut twig

A. Terminal bud in early stage of opening.
B. Leaf scar.
C. Axillary bud.
D. Lenticels.
E. Terminal bud scale scars.
F. Branch twig with terminal bud at its apex.
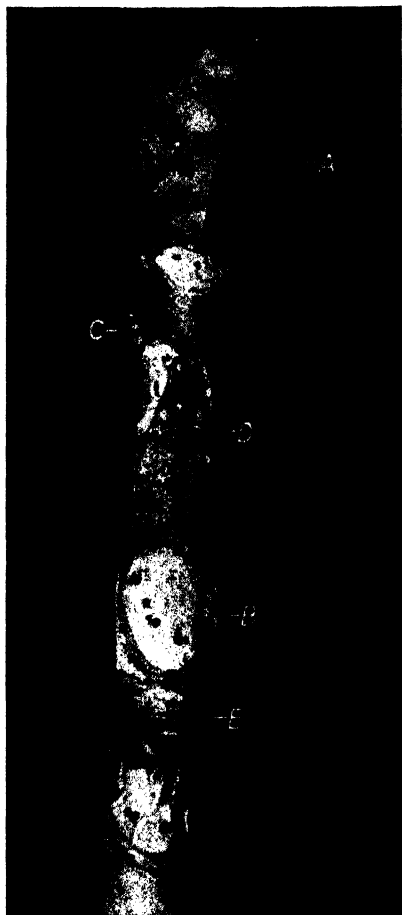
Fig. 41. Terminal portion of horse-chestnut twig

A. Terminal bud, showing bud scales.
B. Leaf scar with vascular bundle scars.
C. Axillary bud.
D. Lenticels.
E. Terminal bud scale scars.

which he is growing. In a plant with an active terminal bud and with slow-growing or dormant axillary buds, the removal of the terminal bud usually stimulates the axillary buds to greater activity, in many cases overcoming their dormancy. Thus, a bushier growth of a plant may be induced by pruning away certain of the terminal buds. In chrysanthemums all buds except the terminal one may be removed, a process called **disbudding,** with the result that the single shoot becomes very tall and erect and the "flower" which develops

from the single bud is much larger than it would be were other flower buds allowed to develop. The elimination of competition among several buds for the food manufactured by the plant places all of the food at the disposal of the sole remaining bud and thus causes it to form an unusually large "flower." Disbudding is a common horticultural practice in the culture of many species of plants.

An examination of the surface of a herbaceous stem shows relatively few structures other than buds, leaves and branch twigs of both vegetative and reproductive nature. There may be **hairs** which are outgrowths of epidermal cells, **stipules,** small projections of
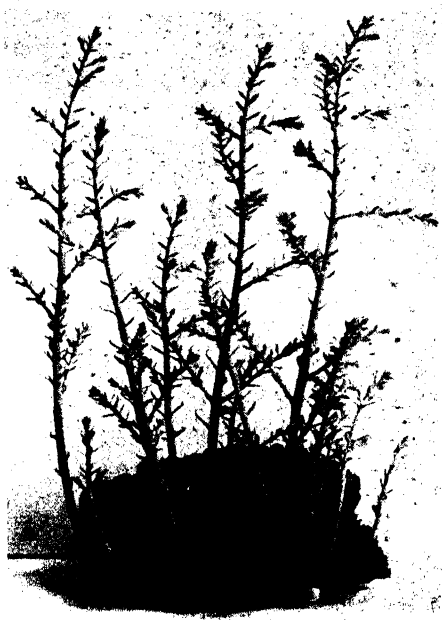
Photo by Missouri Botanical Garden

Fig. 43. Shoots developing from adventitious buds on the burl of a redwood tree.

tissue at the point of juncture of leaf stalks with the stem, and occasionally **spines** which may be modified twigs, leaves, hairs or stipules. In the woody twigs of trees and shrubs, however, other structures in addition to the above-mentioned features there are present (Figures 41, 42). These are **lenticels, leaf scars, bundle scars, bud scars,** and **twig scars.** Lenticels are tiny pores which are scattered over the surfaces of woody twigs. They are usually surrounded by a margin of raised cork tissue; through the lenticels an exchange of gases between the tissues of the stem and the external air occurs. Lenticels are usually circular or nearly so in shape, although in some plants, for example, the cherry and peach trees, they are transversely elongated slits. Leaf scars are sometimes apparent in annual plants, if some of the leaves fall away, but they are especially conspicuous on woody twigs in autumn and winter. A leaf scar is a mark left when a leaf stalk breaks away from the twig. Leaf scars are variable in form in different species; common shapes of leaf scars are narrow crescents, U's, V's, and sometimes circles and triangles. In the twigs of the Chinese tree of heaven, the leaf scars are

Fig. 44. Sprouts from adventitious buds on catalpa stump.

roughly triangular in shape, with sides about one-half inch long. In other woody plants, such as Hercules' club, the leaf scars are narrow and elongated transversely, frequently attaining a length of more than an inch. In most cases, however, leaf scars do not exceed $\frac{1}{4}$ to $\frac{1}{2}$ inch in length and are most commonly U-shaped or V-shaped. Bundle scars appear as tiny raised dots on the leaf scars. Bundle scars are the broken ends of **vascular bundles** (conducting strands) which extend from the twig into the leaf stalk. When a leaf falls, these bundles are broken across at the point of separation of the leaf from the stem and thus are visible in cross-sectional view within the leaf scars. The number, size and arrangement of bundle scars varies in different species of plants. Bud scars are rings of small, narrow scars left by the bud scales as they fall away from the base of an opening bud. These bud-scale scars are inconspicuous individually, but the ring which the several scars form is readily visible. Most of these bud scars are left by terminal buds and each of them marks the place at which a terminal bud began its development in a spring season. Since a new terminal bud develops each year from the previous terminal bud of the twig and opens in

the following spring, the number of these bud scars on a twig indicates the age of the twig. By counting back from the apex of a stem the number of bud scars present, it is possible to determine the age of any section of the twig. Twig scars are usually circular in outline, are frequently slightly concave, and occur in the axils of leaf scars. They mark the points of juncture of fallen branch twigs with the main twig. If the branch produces a flower instead of a vegetative twig, the scar left by the fallen fruit (a fruit develops from a flower) is called a fruit scar. Such a scar is similar in form and position to the scars left by vegetative

Photo by Missouri Botanical Garden

Fig. 45. Self-pruning in sycamore.

twigs. In many species of woody plants, there is a regularity in the rate at which certain of the twigs and branches fall away from the branches from which they arise. This phenomenon is termed **natural** or **self-pruning** (Figure 45) and is especially noticeable in dense stands of trees, the most heavily shaded twigs and branches of which fall away while they are still relatively young.

As woody stems grow in diameter the smooth, young outer bark is split, partly by the formation of new tissues, by the rapid cambial growth inside the bark. With the cracking of the young bark and the growth of new cork layers, the surface of the branch becomes much roughened in most species of trees and the various structures described above are no longer visible. In some species, such as birch and willow, the bark remains rather smooth, even on old parts of the stem and some of the structures characteristic of the younger twig surfaces — lenticels principally — are still visible on the bark of old branches. The relatively smooth bark of birches has been extensively used by semi-civilized races, such as the American Indians, in the construction of canoes and as a material upon which drawings and inscriptions could be made.

3. SPECIALIZED STEMS

There are in many species of plants stems which differ markedly in structure and function from the common types of aerial stems described in the preceding section. Such stems are termed **specialized** or modified stems.

Most common of these specialized stems are underground, or subterranean stems, of which there are four principal kinds: **rhizomes, tubers, bulbs,** and **corms.** A rhizome is a horizontal stem which grows at or below the surface of the soil, occasionally with its upper surface exposed to the air. Rhizomes, and occasionally other types of specialized underground stems, frequently resemble roots superficially; they are, however, true stems, for they have nodes, internodes, buds, and often leaves. Leaves and buds occur at the nodes of rhizomes, as do also adventitious roots which grow out usually from the lower surfaces of rhizomes. Rhizomes are sometimes slender, as in quack grass, or much enlarged by abundant stores of food, as in iris. The chief functions of rhizomes are reproduction and food storage. Most rhizomes are perennial and thus increase in their length year after year, sending up new plants, or at least new branches at their nodes. If such rhizomes are separated into pieces, as may happen in hoeing or plowing, each segment is able to develop into a new plant and thus increase greatly the number of plants. Because of this behavior and also because of the fact that when rhizomatous weeds are pulled up, fragments of their rhizomes often remain undetected in the soil, plants with stems of this kind are very difficult to eradicate. The propagation of many types of garden plants, such as irises and cannas, is almost entirely by separating large rhizomes into small pieces and planting these.

In some plants, the growing tips of rhizomes become much enlarged as a result of food storage. Such subterranean types of stems are called **tubers,** the best known examples of which are the tubers of Irish potato plants. Starch is the most commonly stored food in the tubers, although other carbohydrates, such as inulin, are stored in the tubers of plants such as Jerusalem artichoke. The "eyes" of potatoes are buds; at each node several buds are formed in the axils of several tiny scalelike leaves. The functions of tubers are food storage and reproduction. Under natural conditions, the rhizomes connecting the tubers with the main stem of the potato plant die in the autumn or winter and the tubers, thus left isolated in the soil, are able to produce shoots from their buds the following spring. Potatoes are also artificially propagated by

tuber segments, called "seed pieces." A tuber is cut into segments, each with one or more "eyes." These segments are planted and each produces a new plant from one of its "eyes."

A bulb (Figure 46) is really a single, large, rather globose bud, with a small stem at its lower end and with numerous fleshy scale-like leaves growing from the upper surface of the small stem, from the bottom of which adventitious roots emerge. Thus, the greater portion of a bulb (Figure 47) consists of storage leaves growing from a small, basally-situated stem. Bulbs serve primarily for food storage and also for reproduction. Axillary buds frequently develop in the axils of the
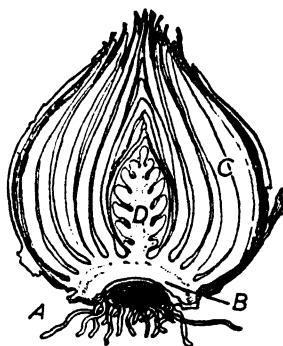
Fig. 46. Longitudinal section of hyacinth bulb
A. Roots.   C. Leaves.
B. Stem.   D. Flower stalk.

scale leaves (Figure 48). These buds resemble the parent bulb, from which they may be separated and used to propagate the species. Among well-known plants the underground stems of which are bulbs, are onion, narcissus, lily, and hyacinth.

Corms resemble bulbs superficially in size and form, but their internal structure differs from that of bulbs. The greater portion of a corm is stem tissue; the leaves are usually thinner and much smaller than those of bulbs. As in bulbs, buds occur in the axils of the thin scale-leaves, and adventitious roots grow from the lower surface of the stem. Corms function as do bulbs for food storage and reproduction. Well-known plants with corms are gladiolus and crocus.

Aerial stems, or portions of them, are frequently modified for the performance of functions unusual in normal types of aerial stems. In various climbing plants, such as grape and Boston ivy, some of the twigs are modified into climbing organs called **tendrils.** In some plants, the aerial stem grows in spiral, rather than erect, fashion about a suitable solid support; such stems, termed **twiners,** are found in the morning-glory and sweet potato. Creeping stems which grow hori-

Fig. 47. Longitudinal sections of bulbs, showing roots, a small, compact stem, and growing from it a number of leaves with thickened fleshy bases. In the center of the bulb is a young, growing flower stalk.
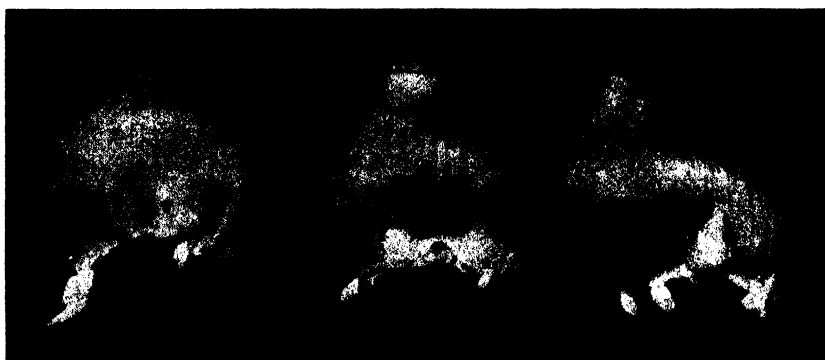
Fig. 48. Bulbs forming on bulb scales of amaryllis.

zontally above the surface of the
soil and which often develop new
plants at their nodes, if these touch
the soil, are called **runners,** or
stolons. These occur in strawberry
plants (Figure 49) and are used
as the common method of propa-
gating this species. The **thorns** of
some plants, such as honey locust
and osage orange, are modified
twigs; these occur in the axils of
leaves and in some cases branch,
as in honey locusts. These thorns
are doubtless of some importance
in discouraging the visits of herbiv-
orous animals. In most species of
cactus (Figure 50), the leaves are
reduced in size, or are transitory,
withering away a few days after
they are formed. In such cases the
stems are green and have assumed
the chief function of the missing
leaves — namely, food manufac-
ture. Cactus stems also store con-
siderable quantities of water. In
some plants, such as onion, **aerial**
bulbs are formed. These are simi-
lar to subterranean bulbs and when
planted in the soil grow into new
onion plants. In those onions which
produce aerial bulbs, the bulbs
form in the **inflorescence** (flower
cluster) in place of flowers and
constitute the principal method of
propagation of various types of
onions. Bulbs, corms, tubers and
other types of underground stems
are essentially perennating organs

Photo by A. S. Colby

Fig. 49. A strawberry plant (a), with
runners (b), and new plants (c), de-
veloped from the runners.

which may remain alive underground for many years, sending up
leaves and flowers at yearly intervals.
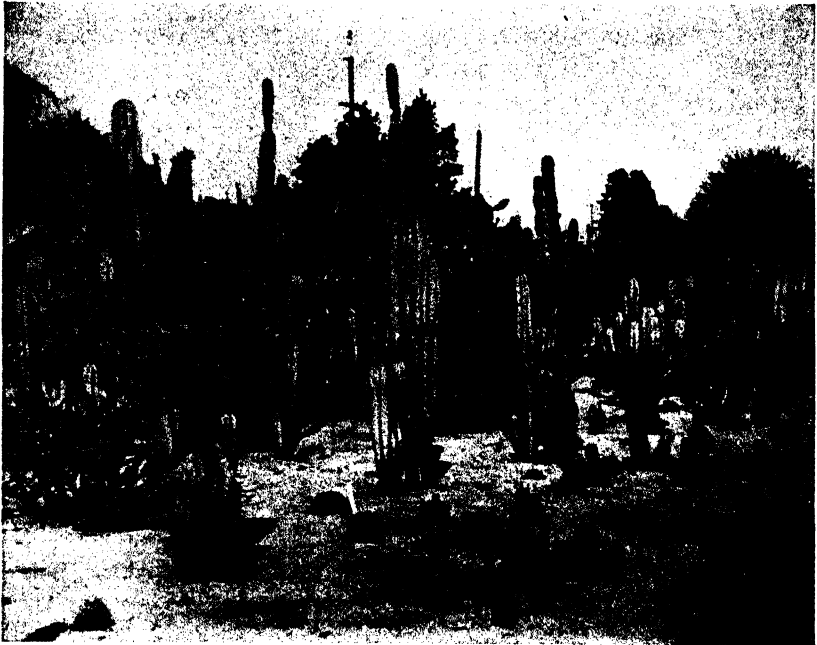
Photo by Missouri Botanical Garden

Fig. 50. A cactus garden in California.

4. EXTERNAL DIFFERENCES BETWEEN ROOTS AND STEMS

The table below presents in summarized form the principal differences between most roots and stems with reference to their external structure and growth habits.

Roots	*Stems*
1. Roots grow downward into the soil.	1. Stems of most plants grow upward above the soil.
2. Roots do not have nodes and internodes.	2. Stems have well-marked nodes and internodes.
3. Root branches arise internally from the pericycle tissue.	3. Stem branches arise externally from buds on the surface of stems.
4. The growing points of roots are covered by root caps.	4. The growing points of stems are naked or are protected by bud scales or young leaves.

5. The characteristic appendages of roots are root hairs.

6. The primary root originates from the radicle of the embryo. Branch roots do not develop in such regular order as do branches of stems.

5. The characteristic appendages of stems are leaves and flowers or cones.

6. The main stem originates from the epicotyl of the embryo, or in part from the hypocotyl. All branch stems have the same arrangement as the axillary buds from which they grew.

SUMMARY

1. Stems arise chiefly from the epicotyls (sometimes in part from the hypocotyls) of embryos.

2. The chief functions of stems are:

    a. Conduction of materials from roots to leaves and from leaves to roots and buds.

    b. The production and support of leaves and flowers (or cones).

    c. Food storage.

3. A stem with its leaves is called a shoot.

4. Aerial stems grow above ground, subterranean stems below.

5. Herbaceous stems are soft, usually green, with little tough, woody tissue, and usually not much growth in diameter; they are chiefly annual. Woody stems are tough, with well developed fibers and other types of strengthening cells, are not green, usually show considerable growth in diameter, and are mostly perennial.

6. Stems bear leaves, and in the axils of leaves, buds. The point on a stem from which a leaf or bud arises is called a node. The length of stem between two successive nodes is an internode.

7. Buds which occur at the tips of stems are terminal, those in leaf axils are axillary. Adventitious buds arise in places other than the axils of leaves or the tips of stems.

8. A bud is a convex mass of meristematic tissue, bearing small, lateral projections (leaves). A naked bud is covered only by tender young leaves. A covered bud is protected by tough, overlapping, protective bud-scales which are modified leaves.

9. When one bud occurs at a node, bud arrangement is called alternate or spiral. When two buds occur at a node, the arrangement is said to be opposite. When more than two buds occur at a node, the arrangement is called whorled.

10. Leaf buds produce stems and leaves. Flower buds produce flowers. Mixed buds produce both stems, with leaves, and flowers.

11. The opening of a bud results chiefly from the elongation of its internodes and the growth of its leaves. The apex of a bud is the growing point, the scene of most active growth in a bud.

12. The form of a shoot system is determined largely by the positions and growth activities of its buds.

13. The following additional structures may be found chiefly on young woody twigs:

    a. lenticels — pores in the bark.

    b. leaf-scars — left by the falling away of leaves.

    c. bundle-scars — broken ends of vascular bundles, in the leaf-scars.

    d. bud scars — rings of scars left by the falling away of bud scales.

    e. twig and fruit scars.

14. Examples of specialized stems are:

    a. rhizomes.

    b. tubers

    c. bulbs.

    d. corms.

    e. tendrils.

    f. runners (stolons).

    g. thorns.

The Internal Structure of Stems

IT WAS pointed out in Chapter VII that the growth in length of roots occurs within a few millimeters of their apices and that a microscopic examination of a longitudinal section of a young root shows four regions of characteristic cells — a root cap, and above the root cap, in order, a meristematic region, a region of cell elongation, and a region of maturation or differentiation. In stems, as contrasted with roots, longitudinal (primary) growth occurs through a greater length of the apical portion often extending through several centimeters rather than a few millimeters as in roots. A detailed examination of a longitudinal section through the tip of a growing stem reveals, however, the same characteristic distribution of cells found in roots, with the exception that structures of the nature of root caps are lacking in stems. In a longitudinal section of a stem tip are found an apical meristematic region, and below this, in turn, a region of cell elongation, and a region of maturation or differentiation. The sizes and forms of the cells in these portions of stems are very similar to those in the comparable regions of young growing roots, except that these individual regions in stems are of greater lengthwise extent than those of roots. A bud differs from the growing tip of a root also in that it produces leaf primordia. The cells of the meristematic tissue of a stem tip bud, like those of a root tip, are small and nearly cubical in shape, with dense protoplasm, and small inconspicuous vacuoles. In the region of elongation, the cells are much larger, particularly in the longitudinal direction, with large vacuoles and with their protoplasm in thin layers against the inner faces of the cell walls. Although the cells of the elongation region enlarge at different rates and in different proportions in various places in the young stem tip, thus giving a forecast of processes of differentiation, they vary little in the structure of their walls and their general forms. In the region of maturation the cells are differentiated into their mature forms in accordance with the various functions which they perform in the physiology of the stem. Here are found the xylem, and

phloem, and other primary tissues of the mature stem, from their very first stages of differentiation to their fully matured, permanent condition.

A study of the anatomical features of plant stems furnishes convincing evidence of the inseparability of function and structure in living cells, of the intricacies involved in the integration of physiological activities with the development of the complex tissue systems of stems. In stems are found strengthening tissues, composed of cells with greatly thickened walls of tough, yet elastic cellulose and lignin, conducting tissues with thinner walls in which are present numerous perforations and thin areas (**pits**) which facilitate the transfer of materials from cell to cell, and storage cells with thin walls and large cavities within which water, minerals, foods, and other materials may be stored. Most of the movement of materials through stems is in the direction of the longitudinal axis — that is, upward and downward. Likewise, most of the stresses and strains to which stems are subjected are exerted in the longitudinal direction. The architecture of stems *seems* admirably designed to meet these demands. The conducting cells are elongated parallel to the longitudinal axes of stems and their pits and wall perforations are located in such manner as to make most effective the upward and downward conduction of materials. Further, the strengthening cells are greatly elongated with tapering ends that fit in snugly with the tapering ends of other strengthening cells and are distributed in such arrangements that they provide maximum resistance to the aforementioned longitudinal stresses. Superficial study of the intimate relationships between the structure of these stem cells and the functions which they perform might lead one to the conclusion that stems have developed such specialized tissues to carry out the functions which they normally perform. Such an interpretation is scarcely justified, however, for it endows plants with highly developed mental traits — namely, foresight and inventiveness — and credits them with purposive action. Actually, the fundamental causes of cellular differentiation are unknown; what determines that certain cells become conducting cells, others strengthening cells is a problem which scientific biological research has not yet solved, although some information is available concerning the course of differentiation in certain kinds of tissues. All that we can justifiably say at present about the complexities of structural and functional differentiation in stems is that the structural features of certain tissues frequently enable stems to grow to considerable size and to perform their functions of conduction and support in a highly efficient manner.

It was stated in Chapter VIII that stems could be classified into two rather distinct types — **woody** and **herbaceous.** Within these two main types of stems are found many anatomical variations. There are numerous types of both herbaceous and woody stems, with reference to the relative extent, positions, rates of growth, and kinds of tissues present in them. It is both inappropriate and impossible, because of lack of space, to consider in a book of this type, the intricacies of structure of the many varieties of plant stems. In this chapter, the internal structure and development of only the commonest types of stems of seed plants will be described. The student should bear in mind in his study of this chapter that only the stem patterns of greatest frequency among plants are discussed and that they are described as types, without consideration of the minor variations which occur among stems of the same fundamental types in different species.

It is generally believed by botanists that woody stems are more primitive than herbaceous stems. Students, because they commonly think of evolution as always a trend from simple to more complex forms of life, frequently find difficulty in understanding this idea, for woody stems are more complex structurally than herbaceous stems. There is abundant evidence, however, derived from studies of stem anatomy, plant fossils, and geographical distribution that the first kinds of true seed plants on the earth were perennial, woody-stemmed plants and that the annual, herbaceous type of stem is a relatively recent development from the older woody type. In accordance with this widely-accepted modern interpretation, this chapter will describe first the anatomy of woody stems and later the structure of herbaceous stems.

1. THE INTERNAL STRUCTURE OF WOODY STEMS

A. *Gross internal structure*

An examination with the naked eye of a cross (**transverse**) section of a mature woody stem more than one or two years old (Figure 51) shows two major groups of tissues: the **bark** which forms the outer protective layer of the stem, and the **wood**, or **xylem**, which lies inside the bark. In the center of the stem inside the wood there is discernible in some species a small core of **pith.** Invisible to the naked eye but exceedingly important in the life of the stem is the **cambium**, a single layer of meristematic cells in the form of a continuous circle
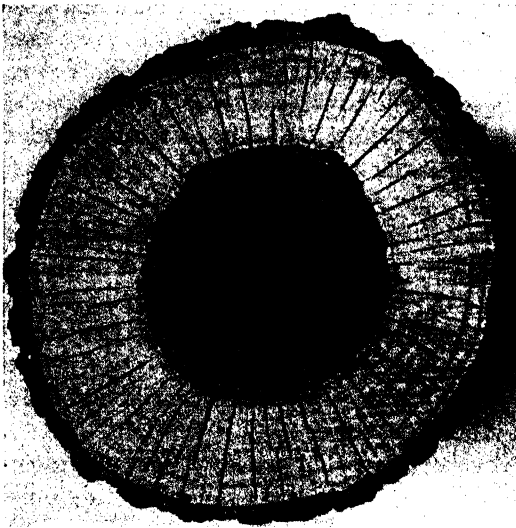
Fig. 51. Cross-section of oak branch showing bark, heartwood (dark, inner portion), sapwood (light portion between bark and heartwood), vascular rays, and annual rings.

Photo by C. F. Hottes

between the wood and the bark (Figure 52). The cambium layer forms new cells transversely or radially in stems, chiefly in the wood, or xylem, and thus causes stems to grow in diameter. The bark is very thin and smooth in young stems but becomes thicker and usually roughened as stems grow older, as a result of the growth activity of the **cork cambium,** a tissue in the outer part of the bark. As stated above, the increase in diameter of woody stems results chiefly from the increase in the number of wood cells; although bark becomes thicker with age, its rate of growth is exceedingly ·slow as compared with that of wood. Thus, as stems grow older, the proportion of wood to bark increases enormously, so that the major part of the volume of the larger limbs and trunks of trees is wood, or xylem. This increase of xylem over bark is in part a result of the fact that all the secondary xylem formed by the cambium is retained within the body of the stem, whereas the outer portion of the bark is slowly and continuously sloughed off.

B. *The primary tissues of woody stems*

    In woody stems of the age described in the preceding paragraphs, the tissues present are chiefly of **secondary** origin — that is, tissues produced by the activity of cambium and cork cambium transversely in the stem, from the latter part of the first season's growth of the·twig through succeeding years. If one examines a cross-section of a twig

Fig. 52. Cross-section of linden (*Tilia americana*) stem

A. Cork and cork cambium (periderm).
B. Cortex and phloem.
C. Xylem, consisting of 5 annual rings. The rings are ring-porous.
D. Vascular rays.
E. Pith.
F. Cambium.

Photo by Triarch Botanical Products
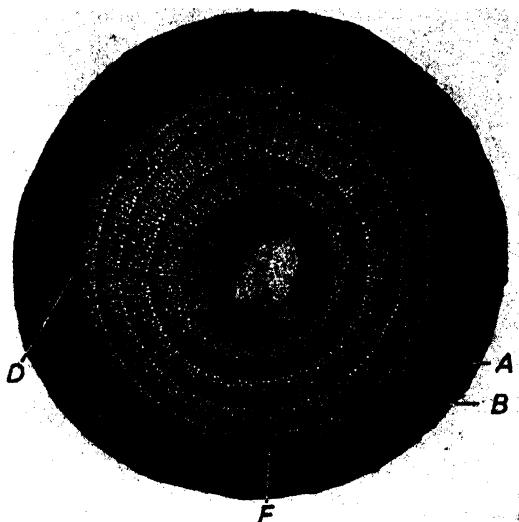
cut in the young part of the maturation region during the early part of the first season's growth of that twig, one finds only **primary** tissues present — that is, tissues formed by growth of the meristematic tissue of the bud and later differentiated into various mature tissues, such as xylem, phloem, etc. These primary permanent tissues are: the **epidermis**, the **cortex**, and the **stelar**, or fibro-vascular, tissues. Figure 53A shows a transverse section of a woody twig with its primary tissues labelled.[1]

The epidermis is a single surface layer of cells, the outer walls of which are usually **cutinized** and thus are nearly waterproof. The epidermis is a protective tissue, which serves chiefly to prevent excessive evaporation of water from the underlying tissues. The cortex varies in thickness in different species of stems and is composed usually of **collenchyma** or strengthening cells, just under the epidermis, **parenchyma** cells which store various substances, and frequently **stone** cells or **fiber** cells, which also aid in furnishing strength and support to the stem. The cortex of woody stems is thus a region of support, of protection for the inner tissues, and of storage. The innermost layer of the cortex in some stems is differentiated into a well-marked **endodermis**; this layer in stems, however, is never as conspicuous as it is in roots. The endodermis is sometimes regarded as a stelar tissue.

[1] The student should refer back to Chapter V and review the subject of tissue structure before he proceeds with his study of this chapter.
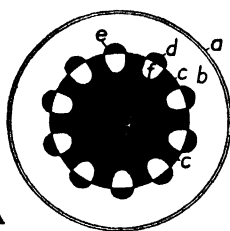
Fig. 53A

Fig. 53. Stages in the development of a woody stem as seen in cross-section

A. Primary tissues of the woody stem as seen very early in the first growing season.
B. The same stem at the end of the first season of growth. Secondary xylem in the form of an annual ring, and secondary phloem have been formed by the cambium.
C. The same stem at the end of three years of growth. There are now three annual rings.

a. epidermis.
b. cortex.
c. cambium.
d. pericycle fibers.
e. primary phloem.
f. primary xylem.
g. pith.

h. secondary phloem.
i. secondary xylem.
  1. springwood.
  2. summerwood.
j. vascular rays.
k. periderm.
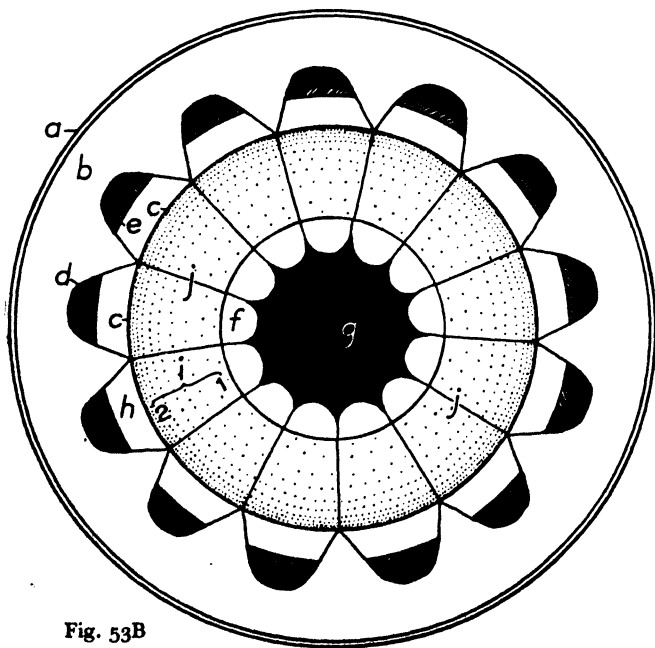
Fig. 53B
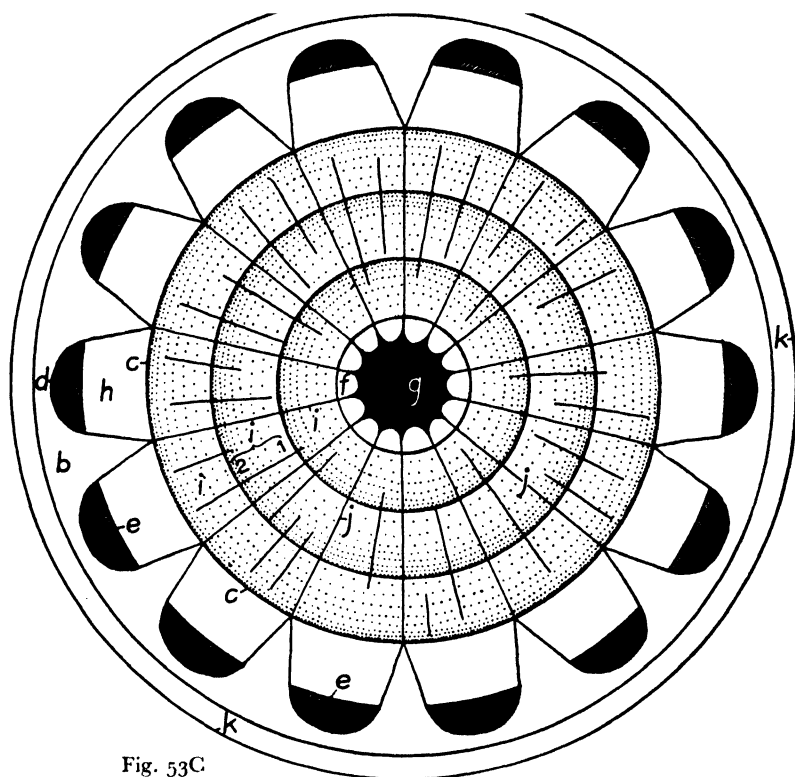
Fig. 53C

The stele, or fibro-vascular cylinder, is composed of several tissues: pericycle, phloem, cambium, xylem (wood), rays, and pith. The pericycle is not readily distinguishable in all stems. It consists usually of parenchyma cells and also of thick-walled fibers. These fibers are long, tough, and pliable and are important not only as sources of strength to the plants in which they occur but are also important to man. Linen and common hemp fibers which are obtained from the flax and Indian hemp (marijuana) plants respectively, are the pericycle fibers of these plants. Linen fibers are used widely in the weaving of fine textiles and in the manufacture of unusually strong threads and cords, such as those used in sewing shoes and in book-binding. Hemp fibers are important in the manufacture of cheaper kinds of twine, such as binder twine, of rope, and occasionally of cheap upholstery, carpets, etc.

The phloem lies inside of the pericycle and consists of **sieve tubes**
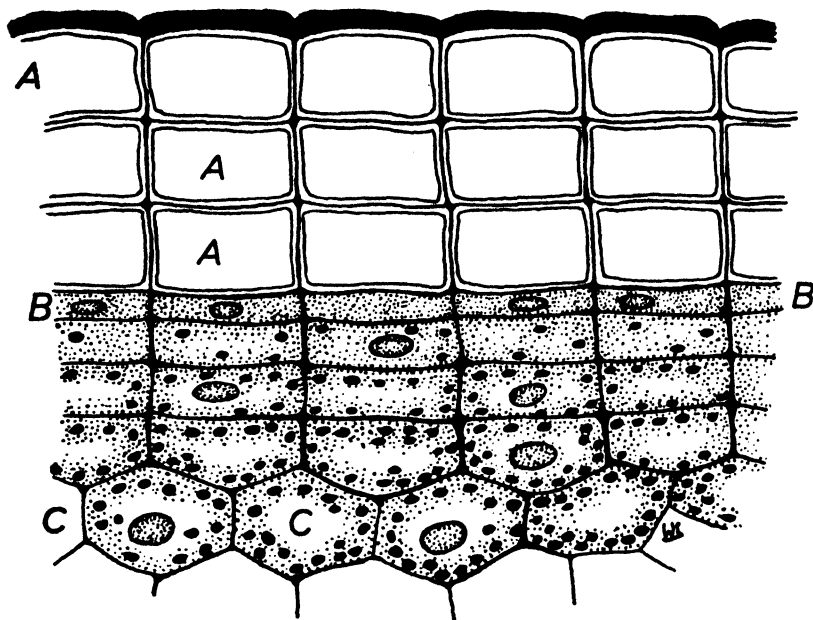
Fig. 54. Periderm and part of the cortex of a young woody twig

A. Cork cells.   B. Cork cambium.   C. Cortex cells.

and their adjoining **companion cells, fibers,** and **parenchyma cells.** The phloem of gymnosperm stems lacks companion cells, and usually fibers, but possesses the other type of cells mentioned. Sieve tubes and companion cells conduct foods manufactured in the leaves downward into the lower parts of the stem system and the roots and upward into the growing points of buds, into developing fruits, etc.; phloem fibers are strengthening cells, and the parenchyma cells of the phloem store foods and other materials. Inside the phloem is the **cambium,** sometimes called the **true** or **vascular cambium,** a single circular row of meristematic cells which are very small, thin-walled, elongated, and more or less rectangular as seen in cross-section. The function of the cambium layer has been described in paragraph A of this section. Inside the cambium is the **xylem,** or wood, which is composed of **vessels** (Figure 59), **xylem (wood) fibers** (Figure 60), **tracheids** (Figure 58), **xylem (wood) parenchyma** cells, and **rays** — types of cells described in detail in the section on tissues in Chapter V. All four types of cells are found in the wood of most angiosperms. In most gymnosperms, however, vessels and wood fibers are not present,
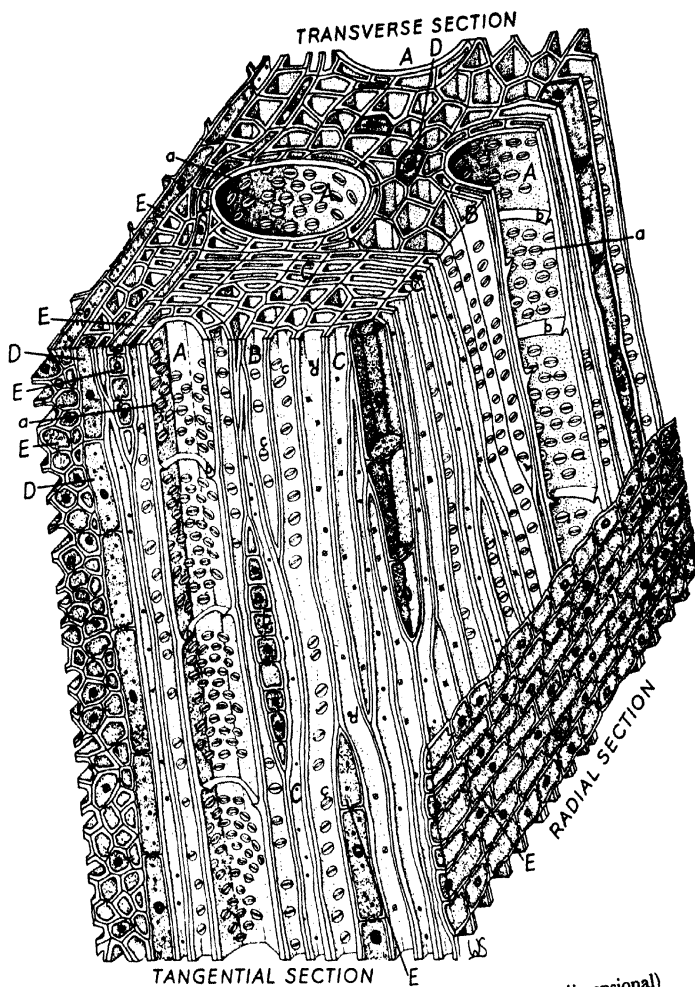
Fig. 55. Microscopic structure of oak-wood (three-dimensional).
A. Vessels: a. pits in vessel walls, b. remnants of end walls of vessel elements.
B. Tracheids: c. pits in tracheid walls.
C. Wood fibers: d. pits in fiber walls.
D. Parenchyma cells.
E. Vascular rays.
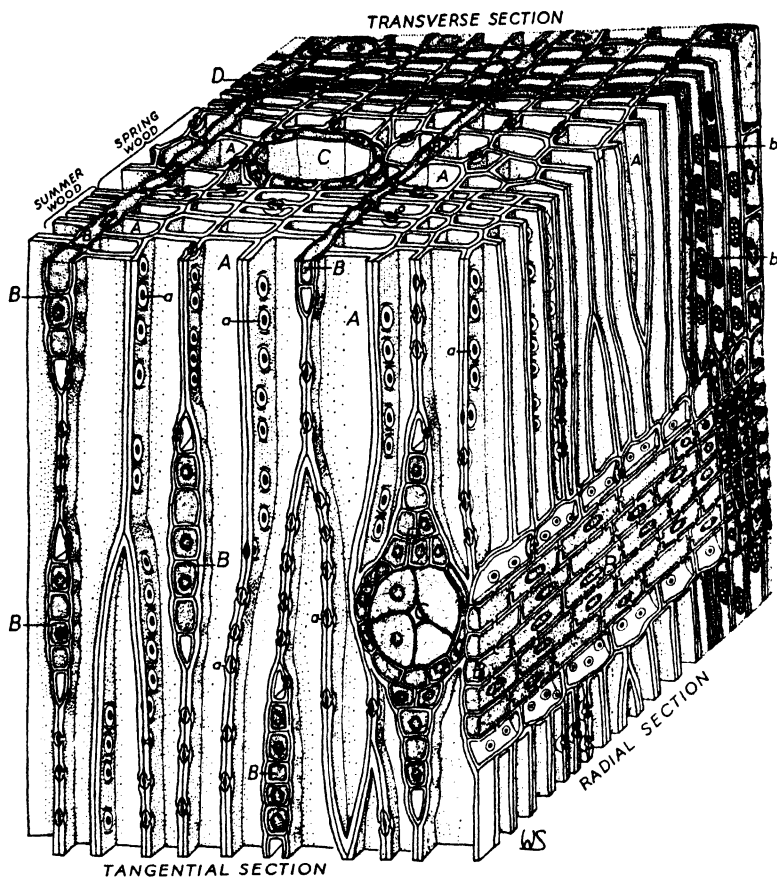
Fig. 56. Microscopic structure of a portion of a pine stem (3-dimensional)

A. Tracheids: a. pits in tracheid walls.
B. Vascular rays.   D. Cambium.
C. Resin canals.   E. Phloem cells: b. sieve plates.

the wood being composed almost entirely of tracheids. There are occasionally other types of structures present in the xylem of some species of woody plants — e.g., the **resin canals** of pines and other gymnosperms. The vessels and tracheids conduct water and dissolved substance and furnish support to the stem, wood fibers function exclusively as strengthening and supporting cells, and wood parenchyma cells are chiefly storage cells. **Pith** tissue, located in the center of the twig, is composed of thin-walled parenchyma cells, the principal

function of which is food storage. In some species of woody plants, the pith is alive only in very young twigs, in others it is still apparent in older branches of considerable size. **Rays** are narrow vertically elongated bands of parenchyma cells which extend transversely from the pith outward to the pericycle, appearing in a transverse section of a young woody twig like the radiating spokes of a wheel.

In the differentiation of the primary tissues of a woody stem from the apical meristem, **primary rays,** extending radially from the pith through the phloem between the vascular bundles, develop. When the cambium forms secondary xylem and phloem cells and thus causes a stem to grow in diameter, it also produces cells which are added to the outer ends of the rays. As a result of this addition of new cells to the rays, the vascular rays continue to grow in length as the stem grows in diameter. The vascular rays usually extend through the xylem and out into the phloem; the portion of a ray situated exclusively in the xylem is called a **xylem ray,** the part extending through the phloem, a **phloem ray.** When a woody stem is relatively young and has not yet grown extensively in diameter, the vascular rays are not far apart. With continued diametric growth of the stem, however, the outer ends of the vascular rays become progressively farther removed from each other. This condition is illustrated in Figure 53. As growth in diameter occurs in woody stems, new vascular rays are produced by the differentiation of certain cells formed by the cambium. These vascular rays, since their formation begins after the tree is several years old, do not extend inward to the pith, but may be seen extending radially across the younger annual rings into the phloem. As a result of the formation of new secondary vascular rays, the distances between the outer ends of the rays do not become appreciably greater as the diametric growth of the stem proceeds, for new rays are continuously intercalated among the older ones and thus a certain proportionality is maintained between the numbers of rays and the total mass of tissues lying between them. The maintenance of such proportionality is doubtless physiologically important, for the vascular rays are intimately concerned with food storage and with radial conduction of foods, gases and other substances and with the nutrition of various living cells in the xylem and phloem; the rate at which such materials are translocated and the quantities of foods which can be stored are limited by the numbers of cells and other structural features of vascular rays and thus the mass of tissue which a vascular ray can serve is limited.
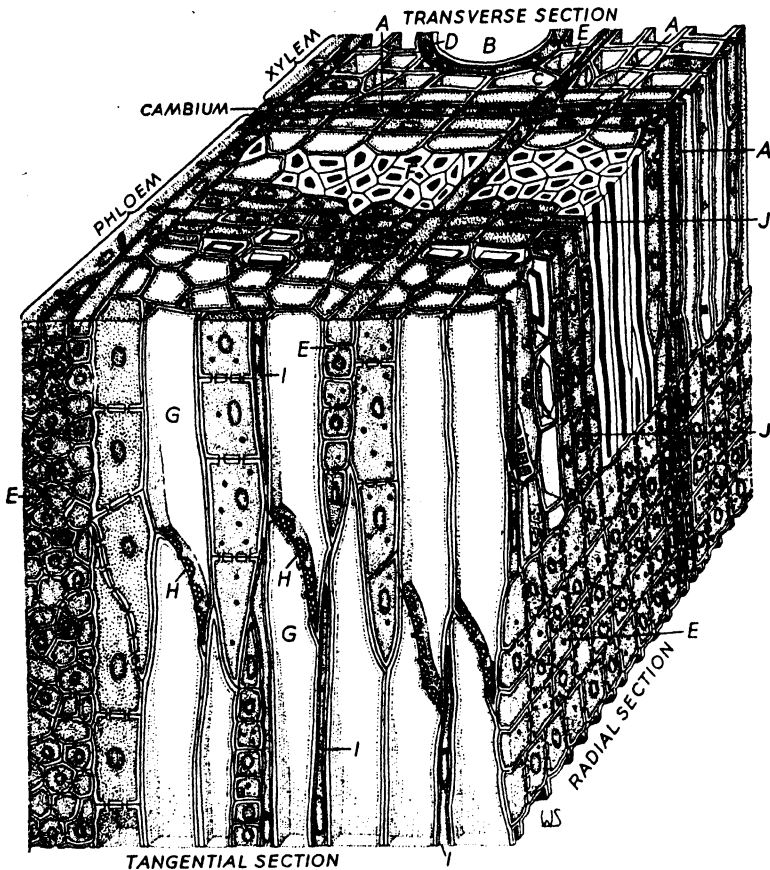
Fig. 57. Three-dimensional view of portion of a linden stem

A. Cambium.
B. Xylem vessel.
C. Wood fibers.
D. Xylem parenchyma.
E. Vascular rays

F. Phloem fibers.
G. Sieve tubes.
H. Sieve plates.
I. Companion cells.
J. Phloem parenchyma.

As shown in Figure 53, the epidermis and cortex are continuous layers of cells in a twig of the type described in preceding paragraphs. In such a twig, however, in the early portions of its first season's existence, the xylem and phloem tissues are often not arranged in continuous layers, as are the epidermis and cortex, but occur as separate groups of xylem and phloem cells. Each of these groups of primary cells is termed a **vascular bundle** and consists of xylem cells in its

inner portion, phloem cells in its outer part, and between the xylem and the phloem, the cambium. This arrangement of the primary xylem and phloem into separate vascular bundles is characteristic of the very young twigs of many woody plants. In some woody species the primary xylem and phloem occur as continuous layers, with no marked separation into bundles. The vascular bundles are arranged usually in a single circle, with the cambium present both in the bundles and extending as a continuous layer connecting adjacent bundles. In the stems of most seed plants, the phloem tissue is situated in the outer portion of vascular bundles, the cambium (if present) inside the phloem, and the xylem as the innermost tissue of the bundle. This

Fig. 58. Tracheids of white pine, showing bordered pits

arrangement is very different from that in young roots, in which the primary xylem and phloem cells are arranged radially in alternate groups, with neither tissue outside nor inside the other.

As stated previously, all of the above-mentioned tissues of a woody twig in the early part of its first season's growth are *primary* tissues — that is, they have been produced as a result of the division of cells in the meristematic region of a bud and of the subsequent enlargement and differentiation of these newly-formed cells. Especially noteworthy in these processes of differentiation is the fact that one of these primary tissues retains the most characteristic feature of the parent tissue from which it developed — specifically, the cambium is a meristematic tissue and possesses the same ability as the meristematic tissue of the bud, the ability to produce, by means of cell division, new cells, and thus to cause growth. The cambium causes growth in diameter and

thus the tissues which it forms are secondary tissues, although the cambium itself is a primary tissue produced by a bud (apical) meristem.

C. *The secondary tissues of woody stems*

After the primary tissues are formed in a young twig in the manner described in part B, little or no further growth in length of this differentiated portion of the stem is possible. The terminal bud which produced these primary tissues, continues its growth through the growing seasons of successive years in woody stems (or is replaced by axillary buds which function in the same fashion), each year forming a new stem segment with its primary tissues as described above.

As stated in the preceding section the primary tissues of a young twig are completed in the first few weeks of the first year's existence of that twig. Later in the first year of its life, the twig begins to grow in diameter as a result of **secondary** growth which usually continues through a number of growing seasons, often for hundreds or even thousands of years. With each season's secondary growth, the twig or large branch or main trunk increases further in diameter (Figure 53).

This secondary growth occurs, of course, as a result of the tangential division of cells of the cambium, which produces towards the inside new xylem cells and on the outside, new phloem cells. The new xylem cells are added on the outside of the primary xylem tissue and the new phloem cells are added inside the primary phloem tissue. As the secondary phloem develops, it presses outward against the primary phloem and frequently crushes the cells which compose it. When the cambium produces new phloem and new xylem, it does so in most species of woody plants along its entire length — that is, secondary tissues are produced by the portions of the cambium in the vascular bundles as well as the cambium cells between adjacent vascular bundles. Thus, these secondary tissues are formed in more or less continuous layers, as contrasted with the separate bundles in which the primary tissues may be formed. The continuous nature of the secondary tissues is usually more noticeable in the xylem than in the phloem. In the xylem and also the phloem of some woody stems, the secondary tissues are merely added to the primary tissues in the vascular bundles, which thus remain separate and distinct throughout the life of the stem. In such cases obviously the secondary tissues are not formed in continuous layers.

The kinds of cells which are formed by the cambium in its divisions are the same as those formed by the meristematic tissue of the bud in

C   B   A   B

C   A   *Photo by O. Tippo*
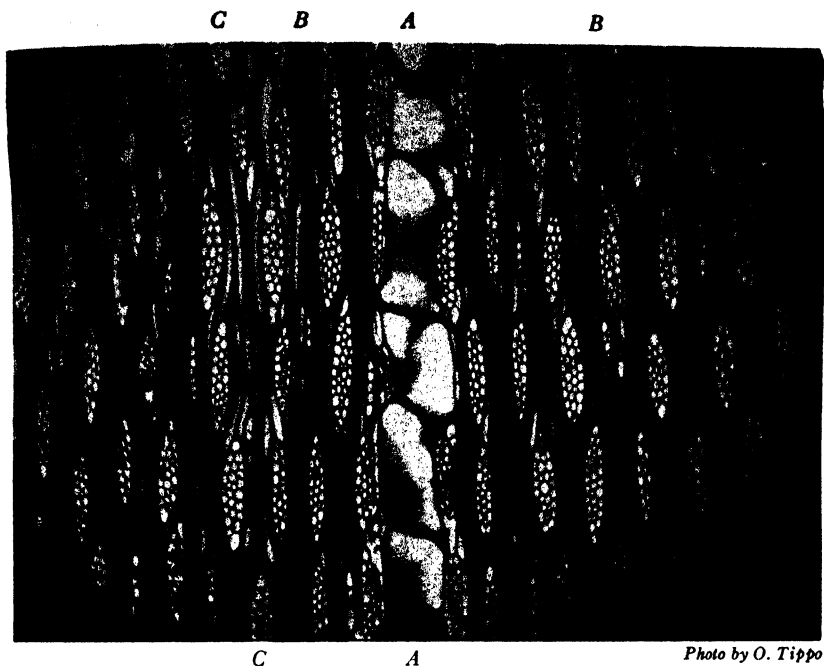
Fig. 59. Photomicrograph of tangential section of wood of a tropical tree (*Holoptelea integrifolia*)

A. Vessel cells, showing pits.   B. Wood fibers.   C. End views of vascular rays.

the primary tissues which it forms — namely, vessels, tracheids, wood fibers, and wood parenchyma in the xylem, and sieve tubes, companion cells, phloem fibers, and phloem parenchyma in the phloem tissue (Figures 55, 56, 57). In its growth, the cambium forms, in addition to secondary xylem and phloem, new vascular rays and brings about the growth in length of the older vascular rays, as described in Section B of this chapter. Although the divisions of cambium cells are chiefly in the tangential direction, producing secondary tissue on the inner and outer cambial surfaces, there is also a certain amount of cell division in a *radial* direction in the cambium, as a result of which the actual circumference of the cambium increases. This radial division of cambial cells, then, enables the cambium ring to expand as it is pushed outward by the xylem with each growing season.

Another group of secondary tissues is produced by the **cork cambium** (Figure 54), a meristematic tissue which frequently has, like the true cambium, the form of a continuous ring in the stem, as seen in
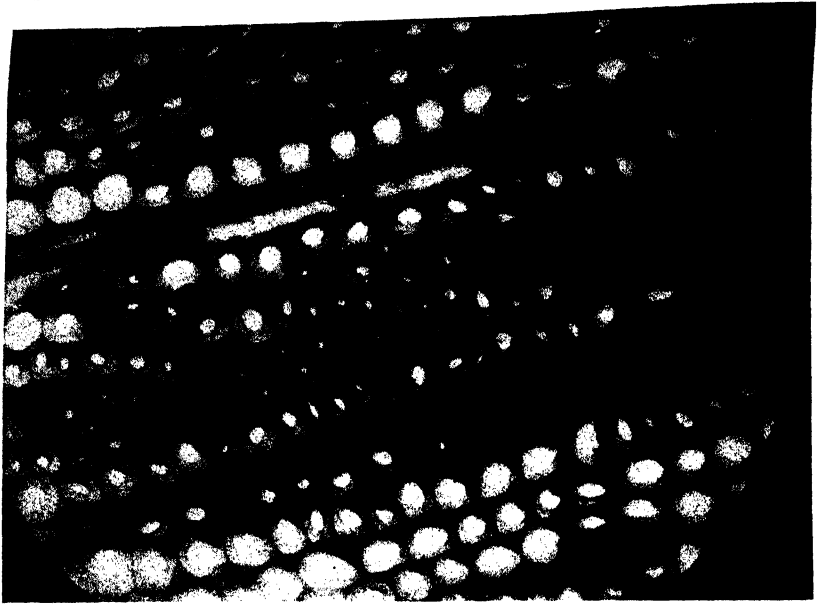
Fig. 60. Photomicrograph of cross-section of wood of a tropical tree (*Paratocarpus venenosa*). Note the thick-walled wood fibers.

transverse section. In some species of woody plants, several layers of cork cambium develop in the outer part of the stem cortex; in such stems, the cork cambium layers are not continuous around the stem but occur as tangentially short bands of growing tissue. The roughness of the outer bark of trees is attributable in part to irregular and unequal rates of growth in the numerous patches of cork cambium. The cork cambium usually develops from certain of the parenchyma cells in the outer portion of the cortex. As these cells become meristematic, they produce tangentially by cell division new cells both on the outer and inner faces of the cork cambium. Those cells formed on the outer surface of the cork cambium become transformed into **cork** cells, which soon become suberized and die. These cork cells prevent the passage of water because of the waxy suberin in their walls and, as a result, the cells of the cortex and epidermis outside the cork soon die because they are unable to get water. These dead cortical and epidermal cells flake away gradually, partly as a result of rain and wind action, partly because they are split by the outward pressure of the expanding tissues inside them. The cells formed on the inner surface of the cork cambium are similar to some of the primary cells of the cortex and are formed in

smaller numbers than the cork cells outside the cork cambium. Thus, as a woody twig grows, the epidermis and outer portion of the cortex, both primary tissues, are cast off and the protection of the internal tissues of the stem against injury, the attacks of parasites, and excessive evaporation, is assumed by the layers of cork cells, which are secondary in nature. This replacement of stem epidermis and cortex occurs in some species of woody plants during the first year's growth of a twig, in other species, not until several years have elapsed.

The term **bark** is used for the aggregation of all tissues outside the cambium. Thus, the bark of a tree consists of secondary and primary phloem, pericycle, remnants of the inner portion of the cortex, the cork cambium, and the cork, named in the order of the location from cambium outward. The term **outer bark** is frequently applied to the cork layers, **inner bark** to the phloem, inner cortex, and cork cambium. Since the phloem of a woody stem is a part of the bark, another function which can be listed for bark is the conduction of substances, chiefly foods, downward into the lower portions of the stem and into the roots.

In the outer bark of several species of trees, as in the cork oak, the cork tissue is composed of very distinct layers of cork cells. These layers are usually annual layers; that is, each layer of cork cells is the amount of cork formed by the cork cambium in one season's growth. As woody stems grow in diameter, the outer layers of cork frequently become split longitudinally and the surface of the bark thus becomes rough. This splitting is caused as stated above, by unequal growth in several cork cambiums and by the fact that the xylem and inner bark continually grow and as they do so exert an outward pressure. The cork cells, being dead, cannot grow to keep up with this internal expansion and consequently they are separated into flakes or ridges by the increasing pressure from within.

The thickness of bark varies in different species of woody plants and on stems of different ages. In most of our temperate zone trees, bark thickness on tree trunks rarely exceeds $1\frac{1}{2}-2$ inches, except in trees of gigantic stature, such as California Big Trees, the bark of which is frequently more than a foot thick near the bases of the trunks.

In the young bark of woody stems, **lenticels** (Figure 61) are present as tiny raised pores in circular or transversely elongated blisters. As stated in the preceding chapter, lenticels are openings through which gaseous exchange between the internal tissues of a stem and the external air may occur. As a rule, carbon dioxide and other gases formed as physiological by-products diffuse outward through these lenticels,
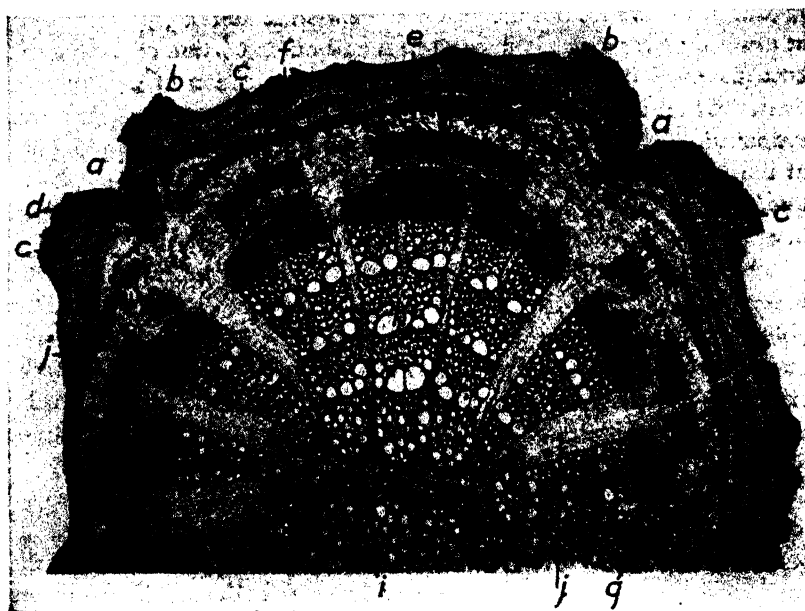
Fig. 61. Cross-section of *Aristolochia* stem

a. lenticel.
b. cork.
c. cork cambium layers.
d. cortex.
e. pericycle fibers.

f. phloem.
g. cambium.
h. xylem, showing 4 annual rings.
i. pith.
j. vascular rays.

and oxygen moves inward from the external air to the stem tissues. The brownish spongy streaks which traverse bottle corks are the lenticels of the bark of the cork oak. Lenticels develop usually at the places where the pores (**stomata**) in the stem epidermis are located. A large number of the lenticels of twigs occurs at or near the outer ends of vascular rays. As stems grow older and the young bark is cracked and furrowed by the growth of the internal tissues, the lenticels are no longer apparent on the surfaces of the bark.

In the temperate zones and also in those tropical regions in which marked wet and dry seasons occur, climatic and other conditions are not suitable for the continued growth of the cambium throughout the year. As a result the cambium experiences alternating periods of activity and of **dormancy**, or relative inactivity. During each of the active seasons, of which there is usually one per year, the cambium forms a new layer of xylem (wood) and a new layer of phloem. Since the
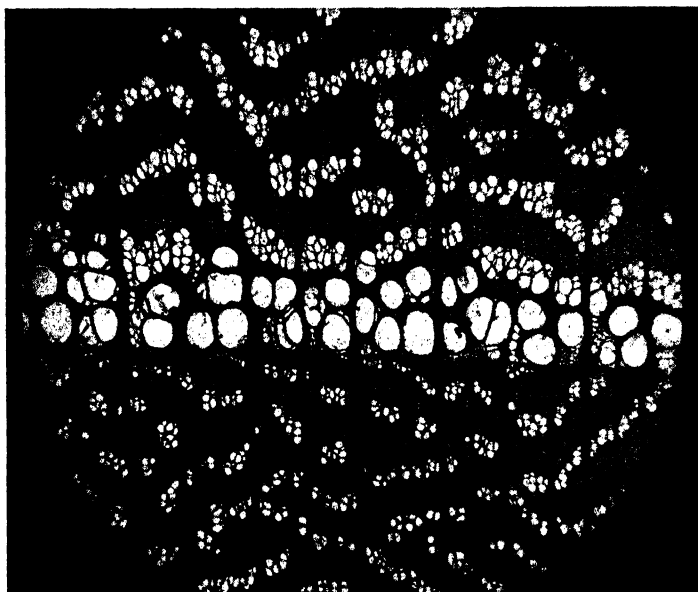
A. Spring-
wood

B. Summer-
wood.

Photo by O. Tippo

Fig. 62. Photomicrograph of a transverse-section of a portion of the ring-porous wood of elm (*Ulmus americana*). The large cells are vessels, the smaller ones chiefly wood fibers. The dark streaks are vascular rays.

amount of secondary phloem tissue formed in one growing season is relatively small, it is difficult, often impossible, to distinguish such seasonal layers in the phloem. In the xylem, however, which increases much more rapidly than the phloem, the yearly amounts of xylem are visible to the naked eye in transverse stem sections as distinct concentric rings, called **annual rings** (Figure 52). A careful examination of each annual ring, in most woody species, shows it to be made up of two fairly distinct bands of xylem cells (Figure 53) — an *inner* portion called the **spring-wood,** in which the vessels and tracheids, especially the former, are relatively large, and an *outer* portion, the **summer-wood,** in which these cells are much smaller in diameter and thicker-walled than those of the spring-wood. As these names imply, the spring-wood is the portion of each annual ring formed in the spring of the growing season and the summer-wood is that formed during the summer portion of the growing period. Spring-wood appears less dense than summer-wood because of its larger cells. The annual ring which is formed during the first season of a twig's secondary growth is the innermost one, the older annual rings being formed in yearly succession, with the youngest

ring immediately inside the cambium. Thus, the summer-wood of an annual ring formed in one year is just inside of the spring-wood of the annual ring formed in the following year. It is because of the alternating bands of spring-wood and summer-wood in the annual rings of a woody stem that the rings are so distinct and thus readily visible (Figure 62). In angiosperm woods, the vessels are largest in diameter of all the cells of the xylem and hence their varying size in spring-wood and summer-wood forms the chief visible distinction between these two zones of each annual ring. In gymnosperm woods, which lack vessels, the tracheids vary markedly in size in the spring and summer-wood and thus form the distinction between these regions.

Since under ordinary conditions, one ring of xylem is formed each year, the number of such rings in a tree trunk and in a branch indicate the approximate age respectively of the whole tree and of the branch. In young twigs in which the first-formed bark has not yet been split, there are thus two methods of determining the age of any portion of the twig — by counting back the number of terminal bud scars from the terminal bud, and by counting the number of annual rings as seen in a transverse section of the twig. The growth of a cambium layer begins as the leaf buds form leaves and continues during most of the period that thè leaves are present during the growing season. Thus, there is a correlation between an annual ring and a single crop of leaves. Occasionally, as result of the complete destruction of all the leaves of a tree by insect attack or drought, a second crop of leaves may be formed in one growing season. In such event, a second ring of xylem is formed by the cambium as the new crop of leaves develops, and thus there are formed in one season *two* xylem rings. For this reason, the number of xylem rings is not always an exact index of the age of a tree, but rather an approximate one. Since the formation of 2 rings in one season is quite rare, however, the number of rings in most cases can be reagarded as indicating accurately the age of a tree.

The widths of the annual rings in a tree trunk or branches are not uniform. Some rings are very wide, others very narrow. The differences in ring-width in the same stem are attributable to the varying climatic conditions which obtained when the various rings were formed. Probably most effective of the environmental factors influencing ring-width is moisture, although such factors as light, temperature, and soil aeration are also important. Annual rings formed in seasons of abundant rainfall are usually wider than those produced in years of drought. The annual rings of small trees shaded by large trees are usually narrow;

when the large trees are cut and sunlight is thus able to reach the leaves of the smaller trees, thereby increasing the rate of food manufacture, the new rings become wider. Frequently trees growing in swamps have narrow rings; if the swamps are drained, thus increasing the oxygen content of the soil, the annual rings produced in years following the drainage frequently become wider. Especially striking in the relation of annual ring-width to these climatic factors is the fact that all individuals of a given species of tree growing under similar environmental conditions produce similar annual rings in the same season. Thus, an annual ring formed in a certain season possesses individuality among the other annual rings in the tree and this individuality of ring structure extends to simultaneously formed rings in other trees of the same species, if they have grown under virtually the same conditions. As a result, the same succession of wide and narrow annual rings may be traced in trees of the same species in the same locality.

The widths of annual rings, then, reflect the environmental conditions which obtained when the rings were formed, and it is thus possible by studying the structure of these rings to read something of climatic conditions of past years. Astronomers have made such studies and have found that there is a remarkable coincidence between sun-spot cycles and climatic cycles, as evidenced by annual rings. Professor Douglass, an astronomer of the University of Arizona, and other investigators, have made extensive studies of this type. In his work, Professor Douglass became interested in some of the old Indian pueblos of the Southwestern United States, the ages of which formed for many years a subject of dispute among archaeologists. Douglass made thin sections of wood beams found in the woods of some of these dwellings and compared them with sections of timbers of known age. By matching the individualistic annual rings in the sections of known and unknown age, he was able to determine the approximate years in which the roof had been cut. Archaeologists generally have accepted the dates which Douglass has assigned by his annual-ring method to the construction of a number of these Indian habitations.

As woody stems grow older, physical and chemical changes occur in the oldest annual rings, those nearest the center of the stem, and gradually proceed outward as the growth in diameter of the xylem increases in successive years. Some of the parenchyma cells which surround the vessels and tracheids begin to enlarge and their protoplasts break through the pits in the walls of these conducting cells. These growths continue to enlarge until they fill considerable portions of the

cavities of the vessels and tracheids. These protrusions into the conducting cells are called **tyloses** and they form plugs which prevent further conduction of water and dissolved substances by the cells. In some trees, tyloses may develop in very young annual rings. The older annual rings are known collectively as **heartwood,** the younger rings situated outside the heartwood constitute the **sapwood** (Figure 51). All conduction in the wood occurs in the sapwood, since the conducting cells of the heartwood are commonly filled with tyloses. The only benefit which heartwood gives to a woody stem is strength and support. In many cases, the heartwood of a tree is burned out or rotted away and yet the remainder of the tree continues to live; so long as the sapwood is intact, conduction of materials upward continues. Trees which have suffered the loss of the heartwood are weakened, however, and are often blown over by winds within a few seasons after the disappearance of their heartwood. As sapwood ages and becomes transformed into heartwood, its living parenchyma and wood ray cells die; thus there are usually no living cells in the heartwood. Various chemical agents usually not present in sapwood, or present in sapwood in small quantities, become abundant in heartwood: **pigments,** which cause the color of heartwood to darken, **resins, gums, tannins,** bitter substances which discourage the visits of parasites, etc. As new annual rings are formed on the surface of the woody cylinder of a tree, the older (innermost) rings of the sapwood are converted into heartwood, usually at about the same rate as the new rings (which of course become the outermost rings of the sapwood) are formed. Thus, the heartwood increases in diameter with the yearly secondary growth of the xylem, whereas the width of the sapwood remains fairly constant in most species. In some kinds of trees, *Laburnum* for example, the sapwood is very narrow, rarely more than 1 or 2 rings wide. In other species, such as certain tropical legumes, the sapwood is frequently 90 to 100 rings wide. The transformation of sapwood rings into heartwood occurs at different rates in various species. In beech, for example, this change is gradual, while in elms it occurs in a single season.

In the wood of some species of trees, spruce, sycamore, and European birch, for example, the wood is fairly uniform and there is no structural differentiation of wood into heartwood and sapwood, although only the younger annual rings function actively in conduction. Tyloses are absent from the wood of some tree species; they are quite rare or absent from the wood of pin oak, for example.

These various chemical and physical changes which result in the

Fig. 63. Fungi growing in sapwood of dead log; note that the heartwood is free of fungi.

Fig. 64. Fungi on sapwood of dead log.

transformation of sapwood into heartwood increase the weight and usually the hardness and resistance to decay of wood. The gums, tannins, and resins (sometimes called **natural preservatives**) are often injurious or poisonous to insects, fungi, and other wood-destroying organisms, the plugged vessels increase the difficulty of penetration of such organisms into the wood, and the absence of recently living cells reduces the amounts of stored food which might be used by these organisms, in heartwood. Thus heartwood lumber is more durable than that from sapwood and is more valuable for construction purposes, particularly for timbers, poles, and boards which are exposed to the outdoor elements (Figures 63, 64).

2. THE INTERNAL STRUCTURE OF HERBACEOUS STEMS

In Chapter III, a brief description of the divisions of the plant kingdom was presented. It was stated that the seed plants, or spermatophytes, are divided into two groups: **angiosperms,** which bear flowers, and seeds enclosed by fruits, and **gymnosperms,** which bear cones, and seeds on the surfaces of cone scales. Each of these groups is further subdivided. All angiosperms are separated into **dicotyledons** and **monocotyledons.** The members of the former group have two **cotyledons,** or seed-leaves, in their seeds, have their flower parts usually in 4's or 5's, and include plants with chiefly **net-veined** leaves; among the

thousands of members of this group are elms, maples, potatoes, beans, roses, poplars, and sunflowers. The monocotyledons are those flowering plants with one cotyledon per seed, with their flower parts in 3's, and with usually long, narrow, **parallel-veined** leaves; common monocots are grasses, such as corn, wheat, and blue-grass, irises, daffodils, lilies, and cat-tails.

The stems of all gymnosperms are woody. Of the dicotyledons, many species, such as elms, oaks, lilacs, hickories, apples, and others, have woody stems, whereas other dicotyledons, such as delphiniums, violets, clover, and snapdragons, have herbaceous stems. Most monocotyledons are herbaceous-stemmed plants; woody species are uncommon among monocots and occur chiefly in the palm and lily families.

The stems of herbaceous dicotyledons and herbaceous monocotyledons differ in certain fundamental structural features and will thus be described as somewhat contrasting types.

In the first section of this chapter, there was emphasized the idea that woody stems are probably more primitive than herbaceous stems and that the latter have probably developed from woody types of stems as a result primarily of the shortening of the life span of stems. What factors actually contributed to the origin of herbaceous-stemmed, annual plants are not known, but botanists have speculated for many years upon this problem and with the aid of geological evidence have constructed a theory which *seems* to explain rather logically the origin of herbaceous from woody stems. In some of the past geological eras of the earth's history, such as the middle Mesozoic, tropical trees of various species grew from the Antarctic regions to Greenland. With the close of the Mesozoic era and the origin of the Cenozoic there began a long period of progressive drying and refrigeration, from the poles of the earth, extending toward the equator. Tropical and subtropical species which formerly extended almost from pole to pole were in part killed off, in part forced to retreat toward the warm portions of the earth's surface, those nearer the equator. It is believed by many botanists that from certain woody species, unable to survive extended periods of drought or low winter temperature, there gradually evolved types of plants which sprouted from seeds and completed their life-cycles in a single growing season, depending upon their cold- and drought-resistant seeds to carry them through a period of climatic conditions which would kill active parts of their bodies. Whether this increased drought and cold actually stimulated the origin of herbaceous-stemmed annuals from woody-stemmed perennials, which could not cope with
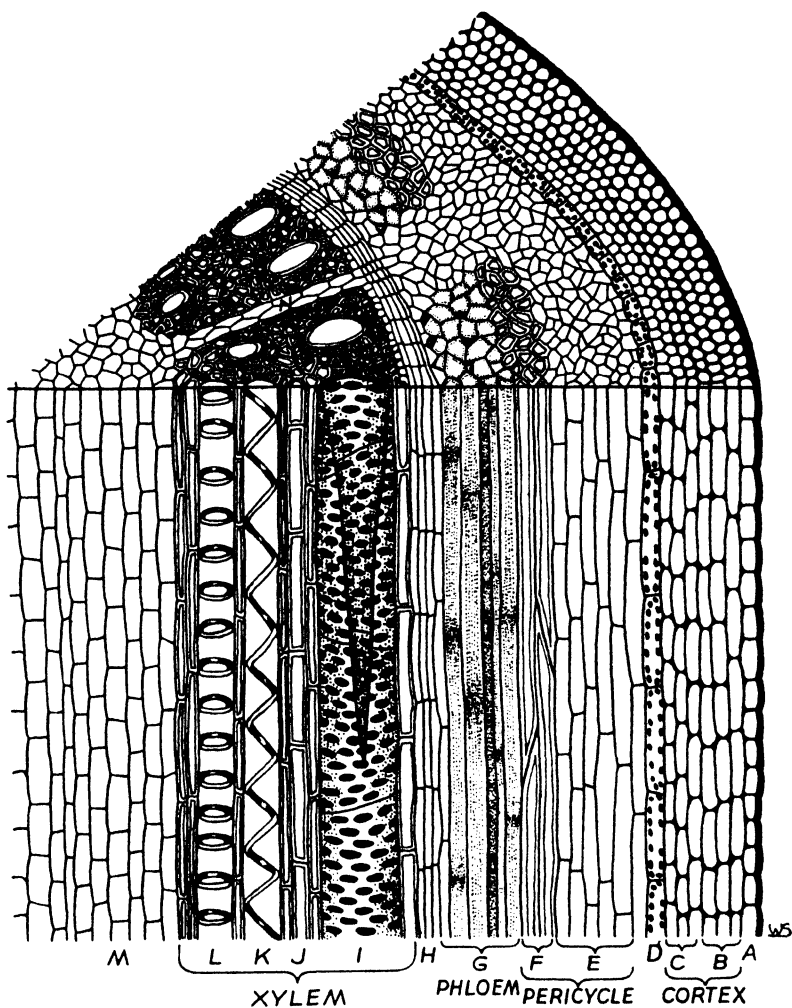
Fig. 65. Diagrammatic 3-dimensional view of a dicot herbaceous stem

A. Epidermis.
B. Collenchyma.
C. Parenchyma cells.
D. Endodermis.
E. Parenchyma cells.
F. Sclerenchyma fibers.
G. Sieve tubes and companion cells.

H. Cambium.
I. Pitted vessel.
J. Xylem fibers.
K. Spiral vessel.
L. Annular vessel.
M. Pith.
N. Ray.

A. Epidermis.
B. Collenchyma cells of
    cortex.
C. Parenchyma cells of
    cortex.
D. Pericycle fibers.

E. Phloem.
F. Cambium.
G. Xylem.
H. Ray.
I. Pith.
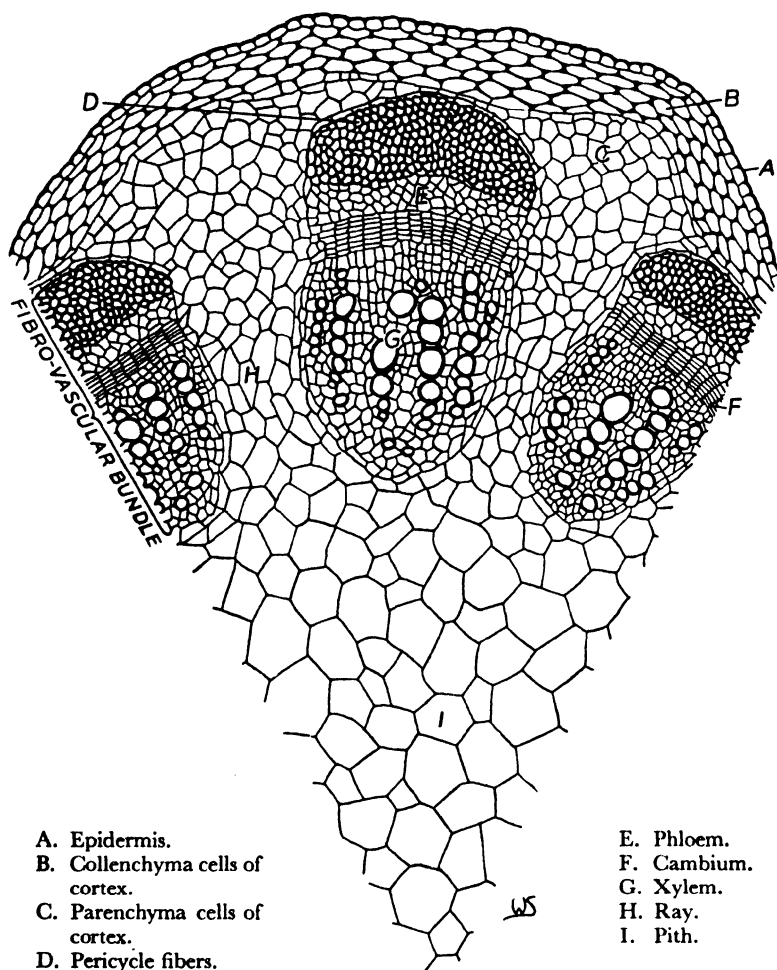
Fig. 66. Sector of herbaceous dicotyledonous stem cross-section (clover)

dryness or cold at certain periods of the year, is not known and probably
never will be. The theory described above is an interesting one, how-
ever, and seems to possess a considerable amount of logic.

A. *Herbaceous stems of dicotyledons*

It has been stated elsewhere that the growth of herbaceous stems is
chiefly primary and that ordinarily little secondary growth occurs in
such stems. This is true both of herbaceous dicotyledonous and mono-
cotyledonous stems.
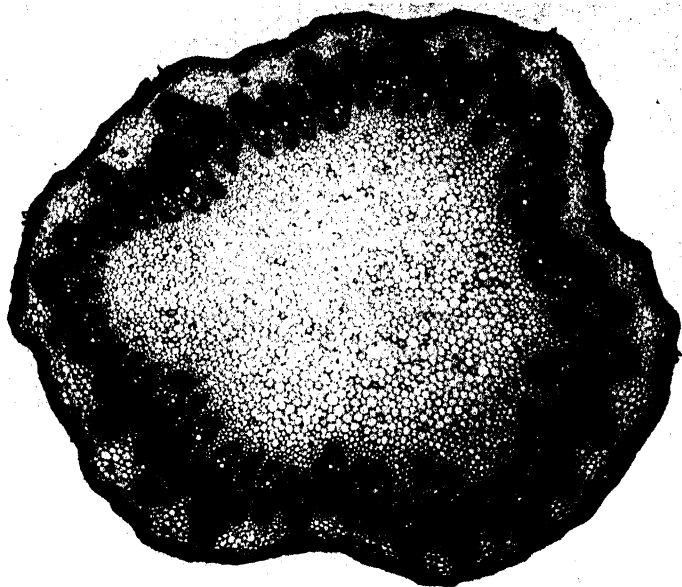
Fig. 67. Photograph of a cross-section of an herbaceous stem showing extensive pith in center, ring of vascular bundles, a narrow cortex outside the vascular bundles, and the epidermis on the surface of the stem.

The herbaceous stems (Figure 67) of dicots are strikingly similar to the stems of woody plants in their primary condition, before the beginning of their secondary growth. In herbaceous dicot stems, as in young woody twigs in the primary state, the terminal bud in its growth forms primary tissues of three types: epidermis, cortex, and stele (Figure 65). The epidermis in herbaceous dicot stems is a single layer of protective cells, similar to the epidermal cells of a young woody stem. The cortex of an herbaceous dicot is much like that of a woody twig, but is usually thinner. The stele is composed of endodermis, primary phloem, cambium, primary xylem, and pith, as in a young woody twig. Pericycle fibers are sometimes present. These stele tissues in a herbaceous dicot stem are arranged either in continuous layers, as in foxgloves, or in the form of separate vascular bundles, as in clover and delphinium stems (Figure 66). In some cases, as in sunflowers, these stele tissues are in the form of distinct bundles in the young portions of the stem system and in continuous layers in older parts. In some herbaceous dicots, the cambium is a continuous layer which extends
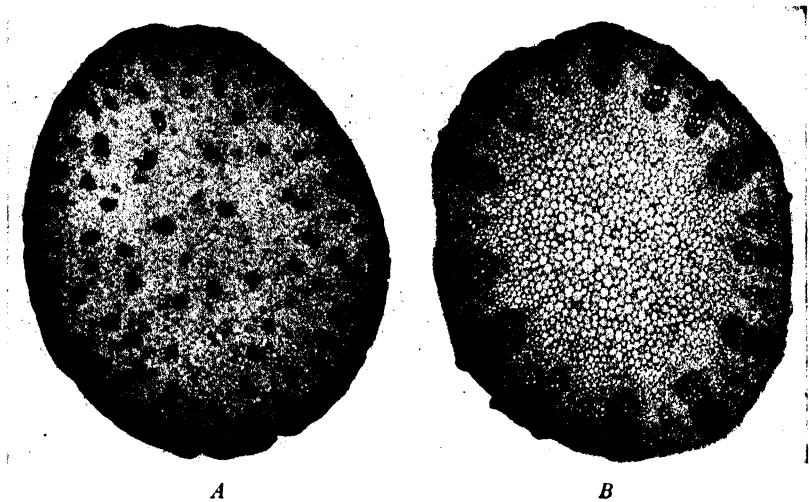
Fig. 68. Photomicrographs of cross-sections of herbaceous stems

A. Monocot herb (corn).   B. Dicot herb (sunflower).

as a complete circle both through and between the vascular bundles, while in other species, cambium cells occur only within the confines of the vascular bundles, not between them.

Thus, in general, the anatomy of herbaceous dicot stems is roughly comparable with that of a young woody twig in its first year. The most conspicuous difference between the two is in the relative activity of the cambium, which in herbaceous dicot stems usually produces little secondary tissue and thus relatively little growth in diameter, whereas in woody stems it is very active, producing large numbers of secondary phloem and secondary xylem cells which bring about a marked yearly increase in the diameter of the stem. Herbaceous stems ordinarily live but a single year, as contrasted with the perennial nature of woody stems, and hence are smaller and much softer than are woody stems. The pith tissue of herbaceous dicot stems ordinarily occupies a much larger proportion of stem volume than it does in woody stems.

Sometimes, under favorable climatic conditions, certain types of herbaceous dicot stems may live longer than one year. In such cases, they may develop considerable amounts of secondary tissue and thus become woody. Castor beans and lantanas grown in northern climates are herbaceous-stemmed annuals, for example, but in the tropics or under prolonged greenhouse culture, their stems become very woody.
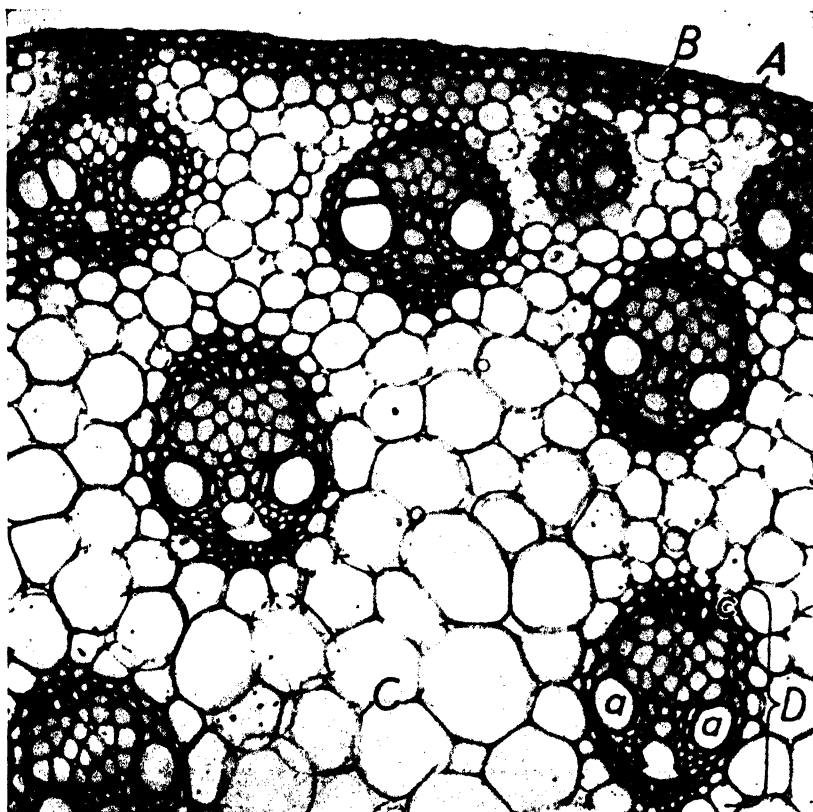
Fig. 69. Highly magnified portion of a cross-section of a corn stem. A. Epidermis. B. Sclerenchyma. C. Parenchyma. D. Vascular bundle. a. xylem; b. phloem; c. bundle sheath.

B. *Herbaceous stems of monocotyledons*

Most monocot species (with the exception of certain palms and members of the lily family) have no cambium tissue in their stems and thus have no secondary growth, their tissues being entirely primary in origin; that is, they all develop from the cells produced by a terminal bud. The xylem and phloem tissues in monocot stems are never arranged in continuous layers, but are in individual vascular bundles, which are usually scattered through the stem, not arranged in a definite circle as in those dicots with their vascular tissues in separate bundles (Figures 68, 69). The vascular bundles are usually surrounded by strengthening cells, which, together with sclerenchyma fibers lying be-
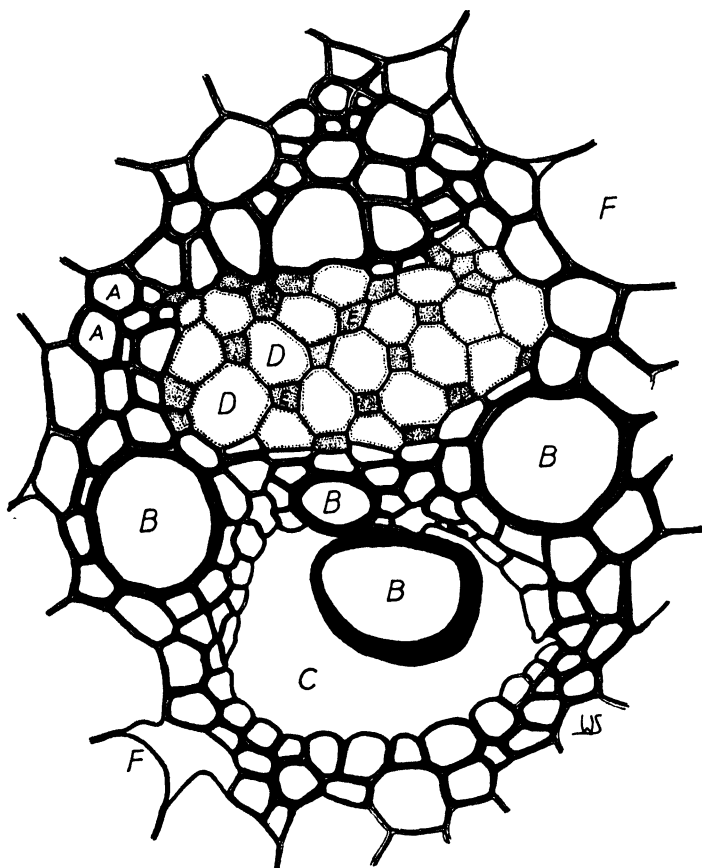
Fig. 70. Vascular bundle of corn stem

A. Bundle sheath.   D. Sieve tubes of phloem.
B. Xylem vessels.   E. Companion cells of phloem.
C. Intercellular passage.   F. Parenchyma cells.

tween the outermost vascular bundles and the epidermis, constitute the major strengthening tissues of monocot stems. In the vascular bundles of monocots, as in those of dicots, the phloem tissue is always in the outer portion of each bundle, with the xylem forming the inner part of each bundle (Figure 70). The surfaces of monocot stems are covered by a protective epidermis, as are the stems of herbaceous dicots. Inside the epidermis and among the scattered vascular bundles is an extensive parenchymatous tissue, sometimes called pith or fundamental tissue. This tissue acts primarily as a storage and supporting tissue.

Because of the absence of cambium in most species, there is relatively little growth in diameter in the stem of monocots. The small amount of radial growth which does occur is caused by the increase in size of primary cells, rather than by the formation of new cells. Obviously such growth is limited by the capacities of these primary cells to expand and is never great.

The palms and certain species of the lily family develop cambium layers, usually in their pericycle or cortical cells. This layer in its growth forms new, secondary vascular bundles and thus may cause a considerable increase in the diameter of such stems, which usually become tough and woody with age. Most monocot stems, however, remain herbaceous throughout their lives.

3. LEAF TRACES AND LEAF GAPS

At each node of a stem, vascular bundles separate from the xylem and phloem tissues of the stem, pass out through the cortex and enter the **petiole,** or stalk of a leaf. These vascular bundles which branch from the vascular system of the stem and enter the petiole are called **leaf traces.** Wherever a leaf trace branches from the conducting tissues of a stem, a small break occurs in the latter. Such an interruption in a portion of stem vascular tissues is called a **leaf gap.** The number of leaf traces which enter a leaf varies in different species of plants; in some species there is only one trace per leaf, in others three, five or even more. These traces continue out through the petioles and as a result of their branching, form the vein system of the leaf. Thus there is a continuation of the vascular tissues of plants from roots through stems into the leaves and likewise into the buds and flowers of stems.

SUMMARY

1. As in root tips, there may be found in buds regions of cell division, cell elongation, and cell maturation, arranged in this order from the apex downward.

2. Woody stems are generally regarded as more primitive, though structurally more complex, than herbaceous stems.

3. A transverse section of a woody stem shows the following regions:
   a. bark.
   b. cambium, just inside the bark.
   c. xylem (wood), inside the cambium.
   d. pith, in the center of the stem.

4. In young internodes of woody stems in their first season of life, the tissues present are largely primary — that is, formed by growth and differentiation of cells from the bud. These primary tissues, in the order of their arrangement, from outside in, are: epidermis, cortex, pericycle, endodermis, phloem, cambium, xylem, and pith.

5. Primary xylem and phloem are arranged in separate vascular bundles, or in a continuous layer, with phloem cells almost always outside the xylem cells, the cambium lying between the xylem and phloem.

6. Secondary xylem and phloem are formed by the growth of the cambium, xylem cells being formed on the inside of the cambium, phloem on the outside.

7. After the early part of their first season of life, woody stems consist chiefly of secondary tissues. Growth in diameter of woody stems is thus brought about by the production of secondary tissues by the cambium. Secondary xylem is produced more rapidly by the cambium than is secondary phloem.

8. Phloem tissue consists of sieve tubes, companion cells, parenchyma, and phloem fibers. Xylem consists of wood fibers, tracheids, vessels, parenchyma, and vascular ray cells. In some plants, one or more of these kinds of cells may be absent from the xylem or phloem.

9. Vascular rays are bands of cells which extend transversely in a radial manner in stems, running through the xylem and sometimes extending outward into the phloem. Vascular rays conduct substances transversely in stems.

10. A meristematic tissue (one or more layers) called the cork cambium develops from parenchyma cells in the cortex and forms cork cells on the surface of woody stems. Large masses of cork cells constitute most of the rough, outer bark of woody plants. The inner bark consists of remnants of the cortex and of phloem.

11. The outer bark is primarily a group of protective tissues, the inner bark a group of food-storing and food-conducting tissues.

12. In the temperate zones and in those parts of the tropics with marked wet and dry seasons, the xylem is formed by cambium in definite rings, usually at the rate of one per year. These annual rings near the base of a trunk indicate the age of a tree.

13. Each annual ring in most temperate zone woody plants consists of a layer of rather large cells (spring-wood) and a layer of smaller cells (summer-wood). The transition from spring-wood to summer-wood is frequently gradual.

14. The structure of annual rings is usually a reflection of climatic conditions (especially rainfall) which obtained when the rings were

formed. Thus a study of annual rings is indicative of climatic features of past years.

15. As woody stems grow older, the innermost (oldest) annual rings die completely, become plugged up, and undergo chemical alterations. These annual rings are known collectively as heartwood. The outermost (youngest) annual rings which contain some living cells and which remain open and able to conduct materials constitute the sapwood.

16. Herbaceous stems grow relatively little in diameter and consist chiefly of primary tissues. The xylem and phloem tissues of herbaceous stems are arranged in distinct vascular bundles, or in a continuous layer.

17. Dicot herbaceous stems usually possess cambium layers and have vascular bundles arranged usually in a single circle or square, as seen in cross-section. Monocot stems, which are mostly herbaceous, usually have no cambium (except in palms and certain other plants) and have scattered vascular bundles.

18. The stems of gymnosperms are woody. The xylem of most gymnosperms lacks vessels, wood fibers, and parenchyma, and consists chiefly of tracheids.

19. Leaf traces are vascular bundles which branch from the vascular systems of stems. Leaf gaps are the interruptions caused by leaf traces in the vascular systems of stems.

The Properties and Uses of Wood; Economic Importance of Stems

THE STEM product of greatest usefulness to man is wood. The suitability of various kinds of wood for the many uses to which this product is put is determined largely by the chemical and physical properties of wood. In addition to these fundamental qualities, there are many other factors, chiefly of economic, political and geographic nature which determine how, when, and where certain specific kinds of woods are to be used. A brief discussion of the chemical and physical properties of wood is valuable in a study of the various economic uses which are made of wood.

1. CHEMICAL PROPERTIES OF WOOD

Water constitutes from 20 to 50% of the weight of wood as it is cut from trees. Immediately after being cut, wood begins to lose moisture and continues to do so until its moisture content may become as low as 3 or 4%. Of the dry materials in wood **cellulose** is the chief constituent, occurring in proportions of 60 to 75% in various kinds of woods. Second to cellulose in quantity is **lignin,** an organic material usually associated with cellulose in the cell walls of wood and responsible in large degree for the hardness of wood. Lignin is present in quantities ranging from 15 to 25% of the total weight of dry wood. Thus, cellulose and lignin together make up 75% or more of all solid materials found in wood. In addition to these two most abundant substances of wood, there are present many other kinds of chemical compounds, of which the following are common: **resins, gums, oils, starch, dyes, tannins, minerals, pectic substances,** and a number of others.

The kinds and relative amounts of these materials present determine how certain woods are to be used. In the manufacture of paper, rayon, cellophane, and other cellulose articles, woods with high percentages

of cellulose and low content of gums, dyes, resins, tannins, etc. are desirable, for such materials lower the quality of these products and must be removed in the manufacturing processes employed. Spruce wood, for example, is especially desired for such products, since it possesses relatively small quantities of these undesired substances and hence can be converted into cellulose products with a minimum of chemical treatments for the removal of impurities. Woods such as log-wood and fustic are used chiefly as sources of dyestuffs, since colored materials occur in large quantities in their wood. Woods with large quantities of tannins, such as chestnut wood and the South American *quebracho* (ax-breaker) wood, are used extensively as sources of extracts employed in the tanning of leather and the manufacture of ink. Sandal-wood, American red cedar, and Guiana cedar wood contain aromatic oils which have exceedingly pleasant fragrances, and they are thus used for the manufacture of fine furniture, cabinets, wall-panels, clothes closets, cedar chests, and cigar boxes. Woods which are shaped into staves for barrels and casks used to store liquids must be free of soluble materials which might alter the flavor of the liquids stored in such containers. The presence of large quantities of tannins, resins, and certain oils increases the durability and resistance to decay of the woods in which they are present and thus in part determine the species of woods to be used for construction work which is to be exposed to agents of wood decomposition.

2. THE PHYSICAL PROPERTIES OF WOOD

Very important among the physical properties of wood is weight, which is expressed usually in terms of **specific gravity** (weight of 1 cc. of a substance compared with the weight of an equal volume of water, which is 1 g.). In general, the hardness and strength of wood are proportional to the weight of wood, heavier woods being harder and stronger than woods of lighter weight. The specific gravity of *wood substance* is greater than that of *wood*, for wood is wood substance, *plus* a considerable amount of air which is held in its cell cavities. Since wood substance never actually exists by itself, but is always in the form of wood — that is, with air intermingled with it, — the specific gravities of woods are of more importance from the botanical and technological standpoints than those of wood substance. The specific gravities of most woods are less than 1.0 — that is, they are lighter than water and will thus float. If wood substance alone could be separated from the air in

it, it would of course sink in water because of its greater specific gravity. As soon as a piece of wood becomes waterlogged (has its air replaced by water) it sinks because its wood substance is heavier than water and it no longer possesses the buoyancy given it by air.

In general, woods of specific gravity less than 0.40 are termed light, those from 0.41 to 0.59 moderately heavy, and those above 0.60 very heavy. Most kinds of wood have specific gravities which range from 0.32 to 0.65. There are of course some woods which are lighter and some which are heavier. South American balsa wood, the lightest commercially-important wood, with a specific gravity of about 0.19, is lighter than cork (sp. gr. 0.24) and is widely used in the construction of airplane models, airplane furniture, and Hollywood movie sets. At the other extreme are lignum-vitae from Santo Domingo and tropical ironwood (*Condalia*) with specific gravities of 1.39 and 1.42 respectively. They are among the heaviest woods known. In the list below are presented the specific gravities of a number of important American woods (in dry, or seasoned condition):

Hardwoods		*Softwoods*	
Ash, white	.55	Incense Cedar	.33
Basswood	.33	Bald Cypress	.38
Beech	.56	Silver Fir	.34
Black Cherry	.47	Douglas Fir	.40
White Cherry	.47	White Pine	.36
White Elm	.47	Sugar Pine	.36
Hickory	.67	Western Yellow Pine	.35
Hard Maple	.55	Redwood	.33
Soft Maple	.44	White Spruce	.32
Red Oak	.57		
White Oak	.61		
Black Walnut	.52		

The list shows that most softwoods have specific gravities of less than 0.41, whereas most hardwoods, with the exception of basswood, vary from 0.44 to 0.67 in specific gravity. The term **softwood** as used here and as interpreted by lumbermen refers to gymnosperm woods — pine, spruce, fir, cedar, hemlock, redwood, etc., while the **hardwoods** are those of broad-leaf, angiosperm trees, such as oaks, maples, elm, beech, ash, and others listed above in the hardwood column.

Another physical property of woods which is important in determining their treatment and ultimate use is their moisture content. The

water content of woods, as stated above, varies a great deal in different species. Before woods can be utilized for construction work, for furniture manufacture, and for other finished wood products, their moisture content must be reduced to 10% or lower. If this process, known as **seasoning,** is not carefully executed, boards and timbers made from the improperly seasoned wood **warp** and **check.** Warping is an undesired bending or twisting of a piece of wood, checking is the formation of splits along the vascular rays. Both are obviously undesirable occurrences since they result in the loss of shape or cracking of objects made of such wood. Seasoning of wood is achieved either by the air-drying of boards in well-ventilated stacks or by drying them in special ovens known as **kilns.** As a result of gradual drying under the mechanical pressure of other boards, the stacked boards dry without change of shape — that is, without warping and usually without checking. Another advantage of a reduction in the moisture content of wood lies in the fact that the susceptibility of wood to attack by fungi and bacteria is thereby decreased.

The use of woods for many purposes places numerous physical strains upon them. It is therefore necessary to know in advance something of the mechanical properties of woods. Several tests have been devised and standardized for measuring the reaction of woods to various types of strains. Among the more important determinations are these: bending strength, that is, the degree to which a board of standard dimensions can be bent by weights before it is fractured; the amount of pressure (termed "compression-strength") which a piece of wood can withstand both parallel to and perpendicular to its grain; the hardness of wood, determined by allowing standardized weights to fall upon blocks of wood or boards and then measuring the distance of penetration of such weights into the wood; resistance to shock, important in measuring the suitability of woods for use as hammer- and ax-handles, etc.; shearing strength, that is, the ability of wood to resist opposite forces which tend to "shear" it or tear it apart; and tensile strength, the resistance to pulling forces in opposite directions. These tests are carried out by various testing laboratories, including the famous U.S. Forest Products Laboratory of Madison, Wisconsin, and their results are available to the general public, to lumbermen, and others whose business or interests involve the utilization of woods.

The strength and hardness of wood are determined by a number of factors, chief of which are: the relative amount of lignin present, the specific gravity (weight), relative amounts of spring-wood and summer-

wood, presence or absence of tyloses, presence or absence of knots, checks, and decay areas, the degree of seasoning, and the relative numbers, lengths, and arrangement of wood fibers. Generally heavy woods, with large numbers of long, tightly packed wood-fibers, with well-developed summer-wood in the annual rings, with large proportions of lignin, and with numerous tyloses in the conducting cells are stronger and harder than woods of lower specific gravity, fewer fiber cells, etc. The principal reason why gymnosperm woods are softer and weaker than most angiosperm woods is the absence from gymnosperm woods and the presence in angiosperm woods of large numbers of thick-walled, heavily lignified fiber cells.

3. THE DURABILITY OF WOODS

The durability of wood, or the degree to which wood can withstand the forces of decay, has already been referred to in the section on heartwood and sapwood in the preceding chapter. It was stated there that timber and boards made of heartwood are normally more resistant to decay than those made of sapwood, because of the presence of tannins, resins, and other "natural preservatives" in heartwood, the lesser porosity of heartwood and the smaller quantities of readily available foods in heartwood. Woods vary naturally in their durability. Among those species considered very durable are red cedar, cypress, black locust, osage orange, redwood, black walnut, and hickory. Moderately durable are Douglas fir, honey locust, oaks, birch, hard maple, spruce, and various pine, while cottonwood, aspen, basswood, firs, and willows are exceedingly susceptible to decomposition. The decay of wood occurs, as a rule only when moisture is present, for the common types of wood-rotting organisms require water for their activities. Bacteria and other types of fungi, molluscs, and insects, such as wood-borers and termites, are the important wood-destroying organisms. Some of these, such as termites, are able to attack and digest wood in the presence of incredibly small quantities of water. Wood-rotting fungi usually require considerable quantities of moisture for their growth in wood. Their fragile threads secrete **enzymes**, or digestive agents, which gradually eat away the hard lignocellulose material of wood. Of all these agents, fungi cause the greatest amount of wood destruction.

Various methods are employed to increase artificially the durability of wood. These methods are of two types: those in which a protective surface layer is applied to wood to prevent the entry of moisture and of

organisms, and those in which the wood is impregnated with chemicals which are poisonous or distasteful to organisms and which thus discourage their growth. Of the former method, paints, varnishes, and lacquers are familiar examples. In the second type of treatment, woods are immersed in a bath, often at high temperature and in partial vacuum, of creosote or zinc chloride. These substances penetrate the wood to some depth and because of their poisonous or deleterious effects, they prevent the entry of organisms. Among wood materials commonly treated with creosote are railroad ties, telephone poles, shingles, fence posts, pilings for wharves, etc. In many cases, the useful period of such timbers is nearly doubled by chemical treatment of this kind.

4. WOOD SURFACES

The appearance of wood surfaces, as seen with the naked eye, varies with different species of wood. Each species has its own characteristic surface markings, by means of which different kinds of woods may be recognized.

Among the prominent features of such markings is the presence or absence of pores (vessels) and the arrangement of these vessels in woods. Woods of pine, firs, spruce, and other gymnosperms are termed **non-porous** because they lack vessels, in contrast to the **porous** woods of angiosperms in which vessels are usually the largest and most conspicuous xylem elements. In some porous woods, as in hackberry, oak, and ash, the pores differ markedly in size in the spring-wood and summer-wood. Such woods, in which the vessels are more or less localized in the spring-wood, are called **ring-porous** (Figure 71). In beech, maple, birch, and other **diffuse-porous** woods (Figure 72), the vessels are more or less equally distributed throughout both spring and summer and are not sharply separated as in ring-porous woods. The presence or absence of pores, and the distribution of the pores within the wood are important characters used to identify various kinds of wood. The presence of pores and their relative sizes and numbers are important in determining the kind of painting treatment required by various types of wood. Woods with numerous, rather large pores ordinarily require a preliminary treatment with a "filler" to plug the larger pores before paint is applied. In the absence of suitable fillers, much paint may be absorbed by porous woods, a wasteful and undesirable process.

The differences in development and in appearance between spring-
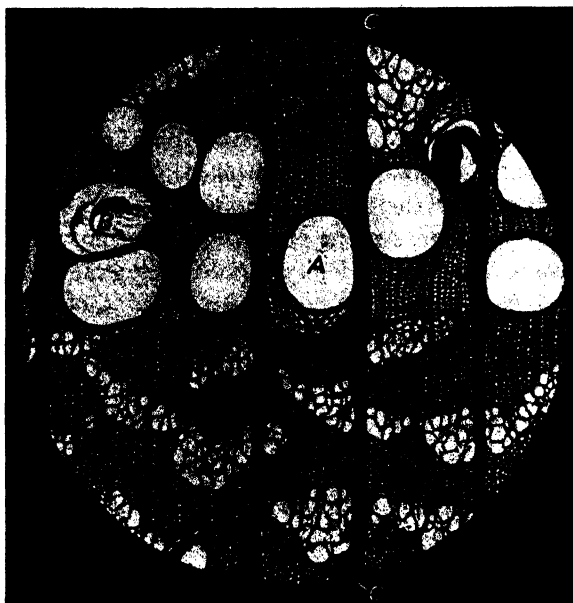
Fig. 71. Photomicrograph of a cross-section of the ring-porous wood of hackberry (*Celtis occidentalis*)

A. Vessels.
B. Vessel with tyloses.
C. Vascular rays.
D. Wood fibers.

Photo by Mary Cox

wood and summer-wood and between sapwood and heartwood have been adequately discussed in the preceding chapter. The differences among these various portions of the xylem are important diagnostic characters of certain woods.

Wood **texture** is an important surface feature of many woods. The fine or coarse texture of woods is caused by the relative size of the component wood cells. Woods with many large vessels are said to be coarse-textured, those with no vessels or very small vessels are called fine-textured woods. The term **grain** refers to the arrangement of the cells, especially the fibers, which constitute wood. Woods are often *straight-grained*, that is, with straight wood cells, arranged in rows parallel to the longitudinal axis of the trunk or branches, occasionally *wavy-grained*, that is, with the individual cells somewhat curved and compressed longitudinally, rather than straight; and *spiral-grained*, in which the wood cells are spirally twisted. Various types of *curly-grains* are due frequently to injuries, the development of adventitious buds, and other types of abnormalities.

The term **wood figure** refers to the characteristic surface appearance of wood. The nature of the wood figure is determined by the arrangement and relative numbers and shapes of the constituent cells. Their figure as it is seen on boards or timbers, on table-tops, wall panels,
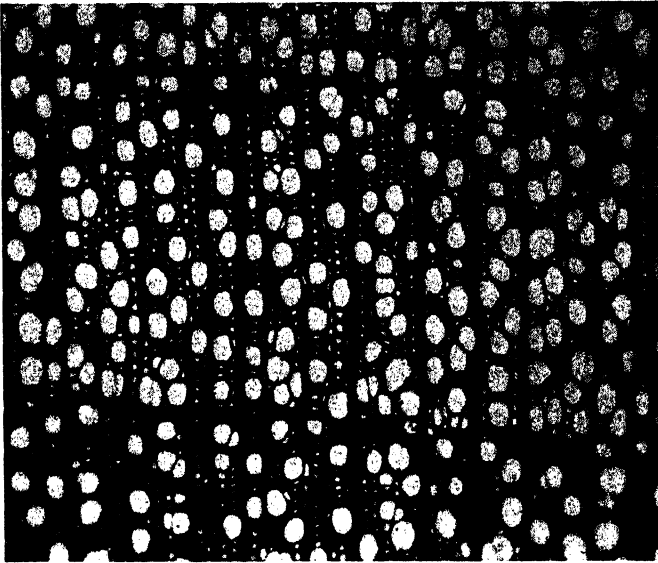
Fig. 72. Photomicrograph of a transverse-section of the diffuse-porous wood of witch-hazel (*Hamamelis virginiana*). The large cells are vessels, the small cells chiefly wood fibers.

etc., varies within the same species of wood, according to the manner in which the boards are cut from the tree (Figure 73). In a **transverse** section, as described in Chapter IX, the annual rings appear as concentric circles and the vascular rays radiate from the center toward the circumference of the wood like the spokes of a wheel. Transverse wood surfaces are seen on cut stumps and on the ends of logs, beams, boards, railroad ties, etc., never as the large surfaces of boards or beams. Wood is not cut transversely into boards because the size of such boards would be limited by the diameter of the tree; furthermore, sections cut transversely, unless they are several inches or more thick, tend to split along the rays and frequently along the annual rings, so that often the latter begin to separate from each other.

The wood surfaces most commonly visible on the larger expanses of boards, panels, beams, etc., are the surfaces of boards cut longitudinally from the wood of a tree. Such longitudinal sections may be cut in two ways (Figure 74): along a radius of the log, that is from the center to the circumference, or, beginning at the circumference, the boards may be cut one after another lengthwise through the tree, tangentially to a radius of the log. A board cut on a radius — that is,
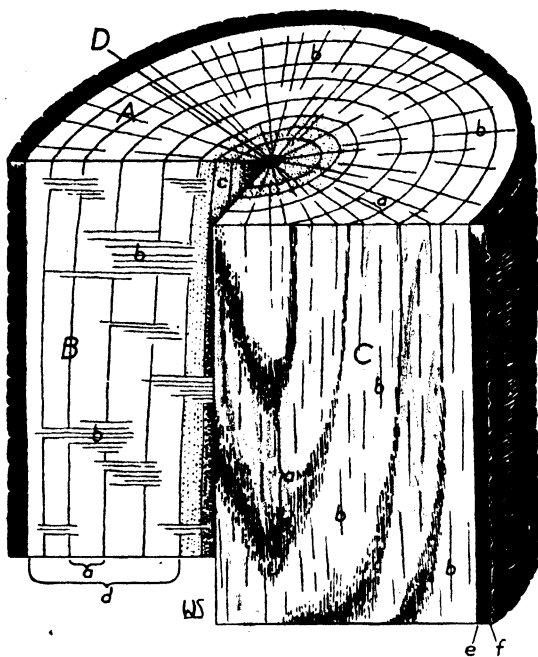
Fig. 73. Three-dimensional appearance of log

A. Transverse section.
B. Radial section.
C. Tangential section.
    a. annual ring.
    b. vascular rays.
    c. heartwood.
    d. sapwood.
    e. cambium.
    f. bark.
D. Pith.
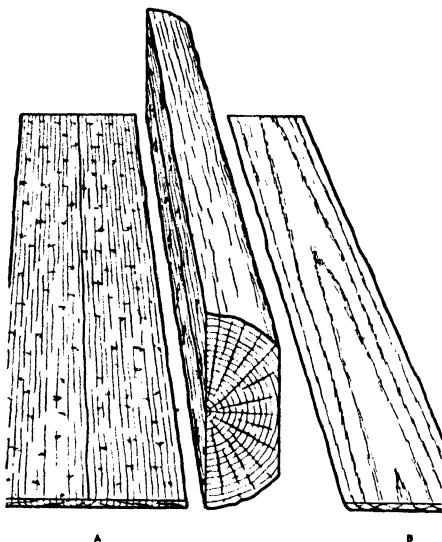
Fig. 74. Quarter-sawed (A) and plain-sawed (B) boards cut from log. Illustrating how quarter-sawed (radially-sawed) and plain-sawed (tangentially-sawed) boards are cut from a log.

By U. S. Forest Products Laboratory

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Fig. 75. Red oak wood (a ring-porous hardwood)

A. Transverse section.   C. Radial section.
B. Tangential section.

parallel to the rays and across the annual rings — is called a **radial** cut or a **quarter-sawed** board, a board cut at right angles to the rays and tangential to the rings is called a **tangential** or **slab** cut. In radial section (Figures 75, 76), the annual rings are seen in *side* view and appear as longitudinal streaks, groups of wide streaks (spring-wood) alternating with groups of narrow streaks (summer-wood); in such a section the vascular rays are seen in *side* view, as horizontal bands, often wavy and irregular in form, running across the annual rings at right angles to the direction of the latter. In quarter-sawed, or radial, sections, the vascular rays constitute the most conspicuous feature of the figure and many woods are quarter-sawed to produce boards with the characteristic ray figure. Because only a small number of perfect quarter-sawed boards can be obtained from a log, quarter-sawed boards are rather expensive as compared with slab-cut boards.

In tangential, or slab-cut, boards, which are cut lengthwise at right angles to the radiating vascular rays, the most conspicuous feature is found in the irregular alternating light and dark colored portions of annual rings. In most boards, the *spring-wood* portions of the annual rings appear dark because their cells are larger and thus reflect less
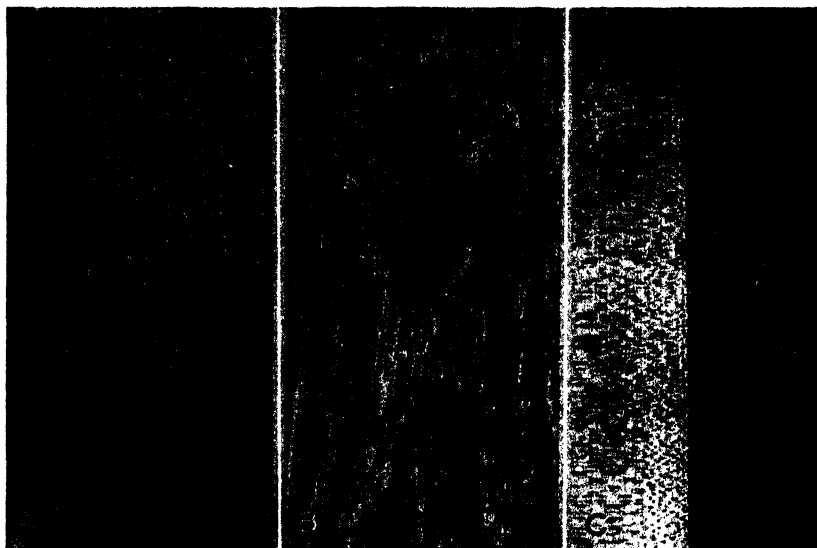
Fig. 76. Yellow birch wood (a diffuse-porous hardwood)

A. Transverse section.
B. Tangential section.
C. Radial section (light portion is sapwood, dark portion is heartwood).

light than do the smaller cells of the *summer-wood* portions, which appear lighter. In tangential sections, the cut ends of vascular rays are visible as narrow vertical streaks at frequent intervals in the wavy, annual ring bands. Of these three types of wood surfaces, tangential sections are seen most commonly because of the fact that the tangential method of sawing a log into boards yields the greatest number of board feet and hence is the most economical method of sawing.

Knots which frequently appear in boards are the basal portions of branches which have become buried in the wood of the main trunk by the growth over a period of years of new annual rings over the branch base. The presence of knots usually weakens the boards or beams in which they occur and thus is not a desirable feature in boards, except those which are used as ornamental panelling.

5. THE USES OF WOOD

The uses of wood are so many that it is possible within the scope of this book to mention only the more important ones. The present

Fig. 77. Workmen stripping cork oak tree of cork. Spain.
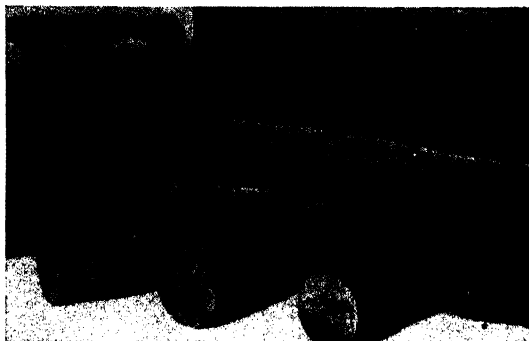
Fig. 78. Bottle corks cut from the cork tissue of the cork oak tree.

Photo by Armstrong Cork Co.

annual consumption of wood in the world is estimated at 56,000,000,000 cubic feet, of which about half is cut in America. The world's greatest yearly per capita use is in the United States, which uses 228 cubic feet per person. Next in order are Germany with 27 cubic feet, France with 26, and Great Britain with 15, per capita. Thus the United States is prodigal in its utilization of wood, doubtless to the point of inexcusable waste. It has been estimated that at present there is cut yearly in our country about six times as much wood as is replaced by normal growth, a truly alarming start on the road to forest bankruptcy.

The chief uses of wood are these: fuel, structural timbers (mine timbers, pilings, ship-masts, etc.), planing mill products (sashes, doors, interior trim, wall panels, flooring), boxes and crates, furniture, vehicles, cooperage (barrels and casks), railroad ties, veneers, shingles, excelsior, and charcoal. In addition to these direct uses of wood, there are many indirect uses of various individual chemical compounds extracted from wood. The process of wood distillation results in the formation of wood alcohol, acetone, wood tar, wood gas, oils, turpentine, and other materials of great industrial value. Wood cellulose freed of other substances present in wood, finds wide use in the manufacture of artificial silk, celluloid, shatter-proof glass, cellophane, photographic film, paper, quick-drying synthetic lacquers, plastics, and numerous other cellulose products.

6. OTHER ECONOMIC USES OF STEMS AND STEM PRODUCTS

The stems of plants furnish many materials, other than woods, which are important in our present civilization. Among these are: fibers (flax, jute, ramie, Indian hemp, and others), tannins, dyes,

perfumes (sandalwood), medicinal substances (quinine, cascara, slippery elm, ephedrine), cork (Figures 77, 78), rubber, chicle (for chewing gum), gums, resins, lacquer, turpentine, balsams, spices (cinnamon, sassafras), and foods. Among the important plants which produce abundant quantities of food for man in their stems are: sugar cane, sugar maple, sorghum, Irish potato, onion, garlic, and ginger.

SUMMARY

1. Most useful to man of all stem products is wood.

2. The most abundant constituent of dry wood is cellulose. Second in abundance is lignin. Other chemical compounds found in wood are resins, gums, oils, starch, dyes, tannins, minerals, pectic substances, etc.

3. Woods vary in their specific gravities from .2 to 1.45. Most softwoods (gymnosperm woods) have specific gravities from .30 to .40; most hardwoods (angiosperm woods) have specific gravities from .40 to .70. The heaviest commercial wood is tropical ironwood (sp. gr. = 1.42), the lightest is balsa (sp. gr. = .19).

4. Heavy woods are usually hard, light woods soft.

5. Seasoning is a process of drying woods so that they will not warp or check.

6. Factors which determine the hardness of wood are lignin content, weight, numbers of wood fibers, presence of knots, decay areas, etc., relative amounts of spring- and summer-wood, etc. High lignin content is usually associated with hardness of woods.

7. Tyloses are masses of parenchyma cells which grow into the cavities of vessels and tracheids and plug them.

8. The durability of wood (resistance to decay) is determined in part by the quantities of resins, tannins, and other natural preservatives present. The durability of wood may be increased by surface painting or by infiltration with creosote, zinc chloride, and other chemical compounds which discourage the attacks of the common agents of wood destruction — bacteria, higher fungi, insects, molluscs, etc.

9. Transverse sections of most woody stems show concentric annual rings, with radially extending vascular rays.

10. Radial sections are cut from logs longitudinally along a radius and show the annual rings as vertical, alternating, regular bands of spring- and summer-wood, with vascular rays extending horizontally across them as flat, ribbon-like structures.

11. Tangential sections are cut lengthwise tangentially to a radius and show irregular, alternating bands of summer-wood and spring-wood, with the ends of vascular rays appearing as streaks in them.

12. Radially cut (quarter-sawed) boards have very fine, rather regular grain.

13. Tangentially cut (slab-cut) boards have coarser, less regular grain. Slab-cut boards are seen most commonly in construction work, because this method of sawing logs is most economical.

The Physiology of Stems and Its Practical Implications

A S STATED in Chapter IV, the principal functions of aerial stems, which constitute the most common type of stems, are the production and support of leaves and flowers, and the conduction of materials upward, downward, and transversely. The production of leaves and flowers by buds has been described in detail, and the strengthening features of stems have been adequately described in the sections on pericycle fibers, phloem fibers, and xylem fibers in Chapter IX. In addition to the execution of these tasks, many aerial stems store foods in their tissues, particularly in the parenchyma cells of the xylem, phloem, pith, cortex, and vascular rays.

1. CONDUCTION OF MATERIALS BY STEMS

The performance of the functions of support, of the formation of leaves and flowers, of food storage, and in some plants, of reproduction, involves processes or forces which are relatively easy to understand. In the case of the conduction (**translocation**) of materials, however, there are many phenomena which have not been entirely elucidated; the problem of the rise of liquids and dissolved substances through stems and of the paths which these substances follow is one of the most intriguing and most complex in the field of plant physiology.

The general term **sap** has been employed both in popular and botanical usage to refer to the water and dissolved materials which move upward, downward, and transversely in stems. Actually, the term is a rather ambiguous one and is used in a variety of ways. Among botanists, the word is applied most commonly to the water and dissolved materials which move upward in the younger annual rings (sapwood) of woody plants, although "sap" is frequently used to refer

to the materials moving in the bark and to the watery juices of herbaceous plants and the softer parts of woody plants. In this discussion, the word will be used as synonymous with the ascending liquid and its solutes in the xylem.

It is known that the chief avenue of the upward transport of water and dissolved substances is the xylem tissue. Various types of experimentation support this view. The phloem and other tissues external to the cambium may be completely cut away without any appreciable diminution in the upward movement of water and solutes. By careful manipulation of a narrow-bladed scalpel, the xylem of a stem can be completely severed with only a slight injury to the phloem. In this case, wilting of the leaves is apparent in a short time and the death of the aerial portions of the plant usually follows. Thus, it is shown that the phloem does not conduct water upward, at least not in sufficient quantities to prevent wilting. If the severed lower end of a stem is placed in a solution of some water-soluble dye, with the remainder of the stem above the liquid, an examination of transverse sections of apical portions of the stem after several minutes or hours have elapsed reveals the presence of the dye only in the tracheids and vessels and occasionally in the parenchyma cells adjoining them. This demonstrates that the upward movement of the colored water has been exclusively through these cells of the xylem. Strasburger, the famous German botanist of the latter years of the nineteenth century, performed experiments similar to these, using trees of considerable size suspended, by means of a derrick, in various solutions. In some of his experiments, he made use of a machine which cut out a ring of sapwood from the tree but left the bark nearly intact. His observations in general led him to the conclusion that the upward path of water and of simple solutes in the water was chiefly the sapwood of the xylem.

It is believed that most inorganic materials (mineral salts) are carried upward in the xylem, for the removal of the phloem and other tissue outside the cambium does not in most cases interfere with the normal supply of these materials to the leaves. There are some plants in which at least a portion of these inorganic substances moves upward in the phloem. It has been demonstrated, for example, that in some trees the removal of the phloem interferes with the movement of nitrogen salts into the leaves. In most plants, however, the greater portion of the mineral salts which reach the leaves seem to move upward through the xylem. In addition to mineral salts, organic materials, such as sugars, are frequently dissolved in the water which rises through the

xylem. Such materials are present in the sap, particularly in the spring in our part of the world, when foods stored in the roots and lower parts of the stem during the preceding growth season move upward and provide the developing buds with the nourishment which makes possible their growth. After the buds have opened and leaves have reached their mature size, relatively little sugar is found in the ascending water. In some plants, when fruits are enlarging, sugars may again be present in the ascending sap, on their journey to the growing fruits.

Although botanists have been able to demonstrate rather conclusively that the upward movement of water and dissolved substances is largely through the xylem, they have not been so successful in explaining the cause of this ascent. Tremendous quantities of water pass out into the air by evaporation from the aerial parts of plants. This evaporated water, plus the amounts of water used for food manufacture and growth, rise through the xylem continuously. The rate of ascent is especially rapid during the growing season when plants are in leaf, and there is also a very slow ascent of materials through perennial stems even during periods of dormancy. Many external factors of the environment, such as air temperature, humidity, and light intensity, are known to influence the rate of sap rise, but the actual internal causes of this movement are not known with certainty. Various explanations have been proposed to account for the ascent of sap, some of them possibly applicable, others patently absurd.

One of the earlier attempted explanations of sap rise was based upon the phenomenon of **root pressure.** It is known that some plants under certain external conditions will exude sap from their stumps, if the aerial portions are removed, or often from broken or cut branches, as in pruned grapevines in early spring, or in the tapped sapwood of sugar maples. In some plants, this sap drips forth slowly, in others it is exuded with considerable pressure which can be measured with suitable instruments. The force which causes this exudation, or "bleeding" is called root pressure. A number of measurements of the root pressure of several species of plants indicates that this pressure is usually not much greater than atmospheric pressure and only rarely exceeds two or three atmospheres. This bleeding is often very copious. Sugar maple trees, for example, exude as much as two gallons or more of sugar-containing juice daily for several days early in spring and some palms have been reported to exude as many as 13 gallons of sap a day, from their severed trunks or leaf stalks. Although root pressure is exhibited by many plants, this force alone is insufficient to

cause the ascent of sap, for its maximum value under normal conditions of growth, about three atmospheres, would be adequate to push sap into the leaves of only herbaceous plants and small trees. Root pressures of more than 12 atmospheres would be required to cause sap to rise in very tall trees, and forces of this magnitude have not been found under normal conditions in the exudation of sap from plant tissues. It is possible that root pressure may be responsible in large part for the rise of sap in herbaceous plants and low woody plants, but it is totally inadequate to cause such rise in large trees. There are other objections as well to explaining sap rise on the basis of root pressure. The severed stems of plants placed with their cut ends in water are usually able to absorb sufficient quantities of water to ensure continued growth and food manufacture in the leaves for long periods of time; in such cases, since there are no roots present, there is obviously no root pressure, and yet the rise of sap continues. Also, there is a lack of coincidence between the periods of the year when root pressure is greatest and when the upward movement of sap is most rapid. Root pressures as a rule are clearly demonstrable only in the early spring when the rate of sap rise begins to increase, when buds begin to swell, and when the stored starch is being digested into sugar, or under conditions which reduce greatly the evaporation of water from the aerial parts of the stem. The period of most rapid sap rise is that portion of the year when the leaves are fully opened and when evaporation from the leaves is most rapid; at such times and under such conditions, however, the exudation of sap, and root pressure are usually not at all apparent; thus, root pressure is evident when the rise of water is slow and is totally absent when the rise of sap is rapid. If root pressure were the chief cause of sap rise, its value would have to be greatest at the time of most rapid sap ascent, and vice versa. The actual situation is just the reverse and thus root pressure seems to be of little or no importance in connection with the upward movement of sap, except possibly in plants of low stature.

Another explanation involves the force of atmospheric pressure. It is known that atmospheric pressure can support a column of water approximately 33 feet high (at sea level), if there is a vacuum at the top of the column, if the column of water is continuous, and if the pressure of the atmosphere is exerted directly on the open surface of the water at the base of the column. It is absurd to attempt to apply this explanation to the rise of sap in plants for several reasons. The presence of an actual vacuum in leaves as a possible result of water

evaporation is not demonstrable, the conducting channels have frequent cross-walls which would interfere with the support of the water columns by atmospheric pressure, and the maximum height to which such pressure could push the sap, namely 33 feet, is far less than the heights of hundreds of species of trees through which sap rises. Thus, atmospheric pressure is a minor, if not completely negligible, factor in the ascent of sap.

When very fine open glass tubes, or tubes of certain other materials, are placed in a vertical position with their lower ends standing in water, ink, or similar liquids, the liquid rises in them to a level *above* the liquid level in the container in which the tubes are standing. The smaller the diameters of the tubes, the higher is the level in them to which the liquids will rise. This rise of liquids in tubes is caused by the capillary or surface attraction between the molecules of the liquid and those of the tube substance. It has been suggested that this force of **capillarity** is involved in the ascent of sap, for the tracheids and vessels of xylem are hollow tubes, roughly similar to the glass tubes in the experiment described above, and their walls are able to absorb and hold water by imbibition. Doubtless, a part of the rise of sap in these conducting elements of xylem is attributable to capillary forces, but the diameters of these tubes and the known forces of capillarity are such, that their force could cause a sap rise of only a few inches, or at most a few feet. Thus capillarity may be regarded as relatively unimportant as a possible cause of sap rise.

Another explanation, to some extent discounted at present, of sap rise is based upon the action of living parenchyma cells adjoining the conducting elements of the xylem. Several plant physiologists have maintained that a pumping action, caused by rhythmic expansions and contractions of these living cells, is detectable in stems and that their pumping force drives the sap upward. This idea, never widely accepted by botanists, received a mortal blow when it was demonstrated that dead stretches of stems, killed by live steam or by poisons such as picric acid, are still able to conduct sap upward in nearly normal fashion. It is extremely doubtful that such pumping action in living cells actually occurs, but it is certain, of course, that water and solutes pass by diffusion from living cell to living cell. It may be that in small herbaceous plants a portion of the sap rise is from cell to cell by diffusion, but in larger plants such passage seemingly has little significance.

The explanation generally considered at present to account most

satisfactorily for the ascent of sap is based upon the idea that sap is *pulled* up through vessels and tracheids by forces operative in leaves, not *pushed* up from below as some of the older, now-discarded theories implied. As stated elsewhere in this chapter, large quantities of water evaporate from the aerial portions of plants, especially from leaves. When the leaf cells nearest the external atmosphere lose water by evaporation, the colloidal materials of their protoplasm are partially dried, and an increase of osmotic pressure in these cells occurs. Since the colloidal materials in protoplasm possess powerful attraction for water, the partly dried protoplasm of these cells absorbs water, chiefly by colloidal imbibition, partly as a result of the osmotic movement of water from adjacent cells with higher water content. These cells in turn, as they suffer partial drying, remove water from cells with higher water content adjacent to them, and thus these imbibitional and osmotic forces, initiated by the evaporation of water from leaf cells, are transmitted from leaf cell to leaf cell. This water deficit in the leaf cells creates a pull on the water in the vessels and tracheids in the leaf veins, a pull which is transmitted downward through the xylem cells of the leafstalk and through the xylem conducting cells of the stem and roots. This pull is transmitted through the water columns of a plant because of the remarkable cohesive power of water molecules, which remain together with such great mutual attraction that tremendous power is required to separate them. The cohesive force of water in columns similar in size to those in xylem vessels has been found to be almost 300 atmospheres, roughly 10 times the pull required to lift sap to the heights of the tallest known trees. The osmotic pressures of the cells of most leaves vary between 20 and 30 atmospheres, more than enough to furnish this pull as water evaporates from them. One investigator has demonstrated very ingeniously the pulling effect of evaporation from leaves by removing a terminal portion, several feet long, from a woody vine and supporting it with its lower end in mercury. When the evaporation of water in the leaves occurred, tensions were exerted on the water columns in the vessels, and these tensions were sufficiently great to cause the mercury to be pulled up into the vessels (because of the adhesive forces between mercury and water molecules) of the stem to a height twice that to which mercury is forced upward by atmospheric pressure.

   This theory, known as the **cohesion theory,** is thus based upon several forces and factors all of which have been shown to exist in the shoots of plants: the evaporation of water from leaves, a water deficit created in leaf cells by this evaporation, the passage of water from the
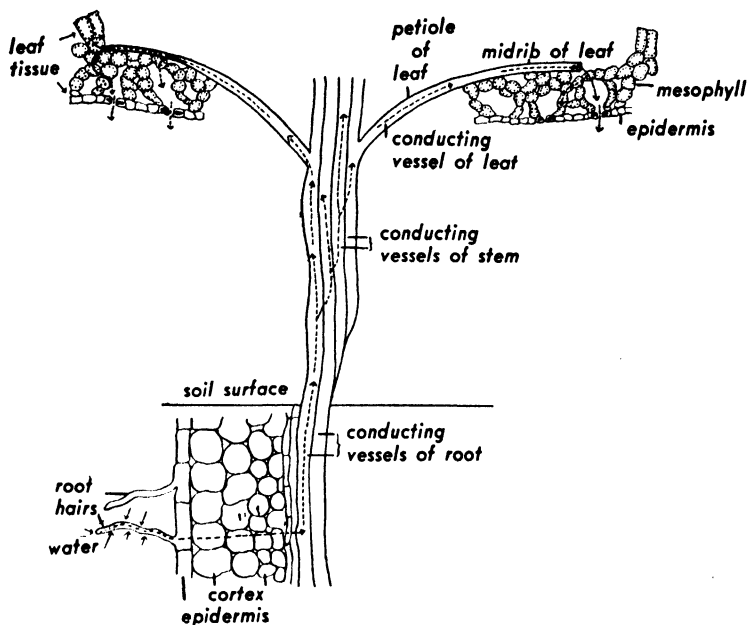
From Plant Life *by Wilson and Haber*

Fig. 79. The passage of water from the soil to the leaves.

xylem cells of the veins into the partly dried leaf cells as a result of colloidal imbibition and osmotic forces, and the transmission downward into the roots, of a pull caused by this water-deficit, a pull dependent upon the great cohesive power of water molecules (Figure 79). There are many indirect evidences in support of this theory. It has been shown repeatedly that negative pressures of as much as 18 to 20 atmospheres exist in the water columns of stems; that is, these water columns are under tremendous tension from above, which tends to attenuate them or draw them out, as a rubber band is stretched when one end is made fast and the other end is pulled with considerable force. These tensions exist in the vessels because under conditions of rapid evaporation from leaves, roots cannot supply water to the xylem elements as rapidly as the water evaporates from the leaves. In plants with rather transparent stems, for example, pumpkin and balsam, the diametric shrinkage of the xylem vessels in the stem under conditions of water tension can actually be observed under a microscope.

It is also demonstrable that on hot, bright days when evaporation of water from leaves is rapid, the stems of many plants, both woody and

herbaceous, actually shrink in diameter, as a piece of rubber tubing will shrink in thickness if one end is closed and suction is applied at the other. The tremendous pull engendered by water evaporation from the leaves creates "negative pressures" or tensions in the water columns, tensions which result in these slight, though definite decreases in stem diameters. Because of these negative pressures air will rush into the conducting cells in which these tensions exist, if incisions are made into a stem. If air bubbles enter a vessel, the upward rise of water in that vessel usually ceases, for the air bubble breaks the water column in the vessel. If the tension in a vessel is lowered, the air bubble may be dissolved and the vessel then resumes its upward conduction of water. When cut flowers are brought into a house, an inch or more of the lower ends of their stalks should be cut off *under the surface* of the water in the flower bowl or vase. This treatment removes the portions of the stalks into which air bubbles entered when the flowers were cut. With the removal of these air bubbles, the upward movement of water is quickly resumed and the flowers will not wilt as quickly as they would if some of the vessels in their stalks were plugged by air.

It should be emphasized that the cross-walls which occur at intervals in vessels and the end walls of tracheids do not hinder appreciably the rise of sap, for these walls are saturated with water and thus masses of water molecules are continuous from cell to cell through these saturated walls. At night, when evaporation from leaves decreases, the negative pressures in stems fall, and a slight expansion in stem diameters is noticeable as the tension in the water columns is relaxed. Further evidence in support of this theory is offered by the structure of xylem cells, the walls of which are usually thickened with rings, spirals, or bars; these thickenings are of such nature that they would seem to prevent the collapse of these cells as a result of the negative pressures in them, in much the same manner as a metal coil in the wall of a vacuum-cleaner tube prevents the collapse of the tube when a "negative pressure" is present inside the tube, rather than to prevent the rupture of such cells by possible upward pressures from below.

Thus the cohesion theory, which is generally accepted by botanists at present, involves chiefly physical forces in its attempt to explain the rise of sap. It should be remembered, however, that the absorption and movement of water and solutes from the soil into the lower ends of the xylem tissues of roots are brought about by the living cells of root epidermis and cortex and that living cells in leaves are involved in the evaporation of water and the transmission of the imbibi-

tional forces occasioned by the partial drying of these cells. Thus, the presence of living cells seems to be necessary for normal sap rise although the chief forces involved in the upward movement of sap are physical forces.

The materials which are dissolved in the rising water in stems are absorbed from the soil and move through the living cells of roots by osmosis and imbibition until they reach the lowermost portions of the xylem vessels and tracheids into which they pass, or if they are foods stored during the preceding year in living root and stem cells, they move from the cells into the conducting elements of the root and stem. The rapid upward passage of water as a result of the forces described above, results in a mass movement of these various solutes along with the water into the veins of leaves.

It is likely that the evaporation-cohesion force is not the only force operative in the ascent of sap. Root pressure may aid in forcing sap upward for some distance in early spring before buds have opened. Capillary forces in the walls of vessels and tracheids, as mentioned above, doubtless play at least a small role in the upward movement of water. In herbaceous stems and perhaps low woody stems, diffusion of water from one living cell to another probably accounts for at least a portion of sap rise. Thus, a variety of physical and vital forces is probably at work in achieving the upward transportation of sap, of which the force produced by evaporation and water cohesion is doubtless the principal one.

The translocation of foods, which are manufactured chiefly in leaves, is principally through the living sieve tubes and, to a lesser extent, through the companion cells of the phloem. The movement of foods in the phloem is chiefly downward. Sugars and various types of proteins are the foods most frequently found in these cells. Several types of experimentation have supplied evidence for the belief that the phloem is the principal food-conducting system of stems. Chemical analyses of xylem and phloem tissues demonstrate that both a greater abundance and a greater variety of foods are found in phloem cells than in xylem cells. Girdling experiments, in which a ring of phloem completely encircling a stem is removed, inward to the xylem, show that conspicuous swellings develop within a few weeks or months immediately above the girdle. These swellings are caused by the accumulation of downward-moving foods which are halted by the interruption of the phloem and which accumulate just above the cut, thus providing nourishment for the rapid growth of stem cells at this point. A complete girdle on the

main trunk of a tree usually results in the death of the tree, for the roots, which are unable to manufacture food, depend for their nourishment upon food from the leaves, and die of starvation when completely severed phloem halts the downward movement of food. It has been observed that certain aphids and other kinds of insects which commonly derive their food from leaves attack the phloem cells of leaf veins more frequently than xylem cells. This behavior is a further indication that more food is found in phloem conducting cells than in those of the xylem.

Recent investigations of translocation indicate that there may be a considerable amount of upward movement of organic materials through the phloem particularly in the spring. During the summer or fall some of the foods moving downward through the phloem are transmitted through the vascular rays to the xylem and stored in the parenchyma and ray cells of the latter tissue. During the early spring some of these foods move upward in part through the xylem, in part upward through the phloem tissue, into which they are carried from the xylem by diffusion through the vascular rays.

The rate at which foods move downward through the phloem is far too rapid to be explained by simple diffusion. The forces responsible for this relatively fast movement are not known. Some plant physiologists believe that there is a mass flow of materials through the phloem, possibly as a result of a pressure gradient from leaves downward. The cross-walls of sieve tubes offer but little resistance to this movement because of the numerous pores in them through which materials may pass.

A notable feature of the conducting systems of stems is the fact that sieve tubes, companion cells, vessels, and tracheids are all remarkably adapted for the translocation of material *vertically* (that is, in the direction of the longitudinal axis of stems) but are almost completely unable to carry materials crosswise (transversely) in stems. Water, foods, mineral salts, and other soluble materials move transversely in stems through the vascular rays, largely as a result of diffusion and rather slow protoplasmic streaming in the ray cells. These rays make intimate contacts with the sieve tubes, vessels, and other cells of longitudinal transport. At such points of contact pits in the walls of the ray cells and those of the sieve tubes, vessels, etc., facilitate the interchange of water and solutes among these cells. This transverse conduction by vascular rays is exceedingly important, for it makes possible the movement of foods from the sieve tubes into the dividing cells of the cambium and

the enlarging xylem cells of the current annual ring, and also enables foods to pass into the various storage cells of the xylem and phloem. There is also movement of gases, dissolved in water, through the rays; carbon dioxide moves outward toward the lenticels, oxygen from the external atmosphere moves inward by diffusion through the ray cells and aids in respiratory processes in cells of the cambium and the living cells of the xylem and phloem.

2. PRACTICAL APPLICATIONS OF A KNOWLEDGE OF STEM STRUCTURE AND PHYSIOLOGY

Floriculturists, orchardists, and others engaged in the practical culture of plants find a knowledge of the basic principles of stem structure and physiology indispensable in their work. Although many men engaged in these vocations do not have a theoretical botanical background, they inevitably learn from practical experience the conspicuous features of stem structure and functions.

The **pruning** of shrubs and trees involves a knowledge of conduction in stems and of the location and activity of the cambium and cork cambium. The chief purpose of pruning is to remove broken or diseased branches and thus to prevent the entry and spread of parasites into the main branches or trunks of trees and shrubs. Pruning is also used to give desired shape to ornamental plants, to control or induce flowering, as in grapevines, and to increase the number of branches on a stem by removing the terminal bud, which in many plants inhibits the growth of axillary buds of the stem at whose apex it is situated. The fundamental guiding principle in proper pruning is to cut away the branch to be removed as close as possible to the main branch or trunk of which it is an outgrowth, and parallel to the longitudinal axis of one main branch or trunk. In order that the growth tissues of a stem may heal a wound, such as one resulting from pruning, phloem cells must be present in such a position that they can conduct food to the healing tissues surrounding the wound. Since the food which moves downward through the phloem cells comes from leaves above, it is essential that there be leaves above the wound in order that food may reach the cambium and cork cambium at the margins of the wound. When a wound is close to a main branch and parallel to it, food moving downward from leaves borne above the wound reaches the cambium and cork cambium around the wound and the growth of protective tissues begins from the margin of the wound and proceeds inward, until the

Photo by C. F. Hottes

Fig. 80. Healing following pruning of tree limbs.

wound is completely healed by a layer of bark (Figures 80, 81). Frequently, pruning jobs are performed carelessly or ignorantly, so that an undesired branch is cut away at some distance from the main branch, as a result of which a stub of several inches is left protruding from the main branch. A wound at the end of a stub is situated in such a manner that healing is usually impossible and the beginning of decay is inevitable. In such a case, the healing of a wound at the end of a stub cannot be promoted by foods passing down the phloem of the main branch, for the movement of foods through this phloem is chiefly *downward* and the wound is too far from the main-branch phloem to receive food for nourishment of the cambium and cork cambium in the stub. The cambium and cork cambium in the stub, then, are out of the main path of food movement of the main branch, and since their only possible sources of food — namely, the leaves borne above them on their own branch — have been removed by the pruning away of that branch, they are unable to obtain food to make possible their production of healing tissue. As a result of the failure of a wound at the end of such a stub to heal, fungi and insects enter the exposed sapwood of the stub and slowly digest their way downward through the wood of the stub into the wood of the main branch or trunk. It is then necessary to cut away the diseased tissue and to pack the cavity with concrete, if the tree is to be saved. Thus, a knowledge of the path of food transport and of the situation of the meristematic tissues in stems is a prerequisite to proper pruning technique. After a pruning job is correctly executed, the surface of the wound should be painted immediately. This treatment protects the wound against the entry of parasites while healing is in progress.

Another practical application of a knowledge of stem structure and physiology is found in **grafting**. Grafting is an ancient and valuable
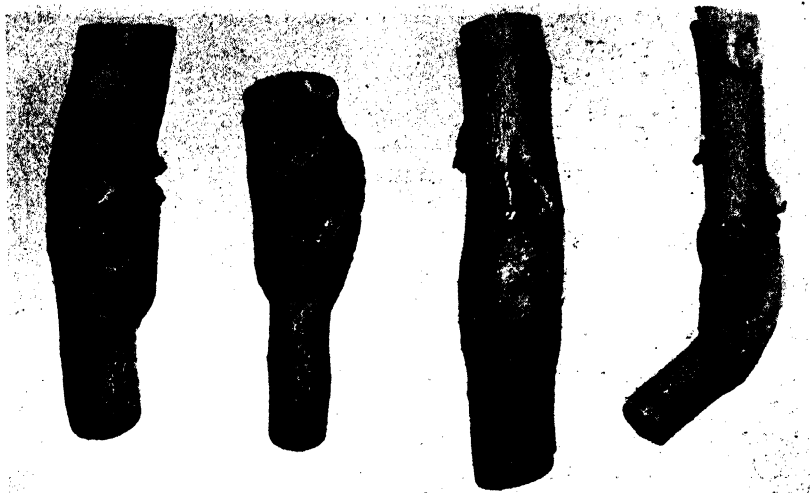
Fig. 81. Marginal healing of pruning scars.

1.   2.   3.

Fig. 82. Treatment of tree trunk cavity (soft maple)

1. The wound is scraped out to remove dead, fungous-infected wood.
2. The cavity is filled with cement in sections to prevent cracking from wind action
3. The same cavity 3 years later, showing marginal healing.

Fig. 83. Treatment of tree trunk cavities (linden)

1. Showing cavity filled with cement and early stage of marginal healing.
2. Same, 2 years later.

horticultural practice in which two freshly-cut stem surfaces are bound together in such a manner that their cells grow together and thus form an organic union between the two stem pieces. The usual types of grafting involve the union of a basal, rooted stem, called the **stock,** and a cutting, called the **scion,** which is united with the stock (Figure 84).

Certain precautions are essential in the making of a successful graft. The stock and scion must be together in such a manner that their cambium layers are in contact, for the growth which brings about the desired union takes place largely in the cambial cells. Further, stock and scion must be firmly bound together with twine or wire to prevent movement which would interfere with the process of tissue union (Figure 85). The grafted region should be covered with a thick layer
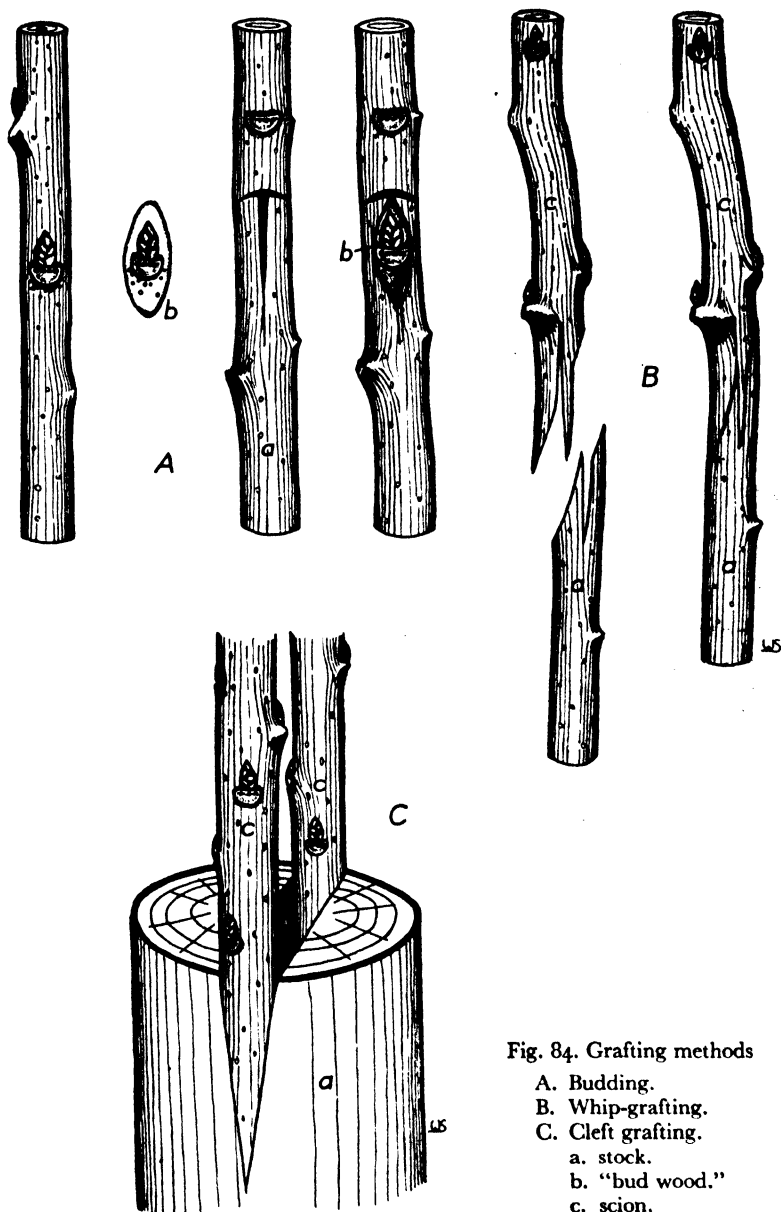
Fig. 84. Grafting methods
  A. Budding.
  B. Whip-grafting.
  C. Cleft grafting.
     a. stock.
     b. "bud wood."
     c. scion.

of grafting wax to prevent the drying out of the tissues and to prevent the entry of fungi. Successful grafts can be attained only when stock and scion are members of closely related species or varieties, for only in closely related kinds of plants are anatomical features and growth habits similar enough to ensure tissue union at the joined surfaces. Thus, apples can be grafted on apples, plums on peaches, tomatoes on potatoes; but apples could not be readily grafted on oranges, nor plums on walnuts, for the plants in these cases do not have enough structural and behavior features in common to produce effective union of their stocks and scions.

There are several methods of grafting, the commonest of which is known as **cleft-grafting** (Figure 86). In this type, a cleft or notch is made in a stock and into the notch is placed the tapering end of a scion, cut to fit the notch of the stock. Another common method of grafting, termed **budding**, employs a scion composed usually of a single bud, with a small amount of adjacent stem tissue. This practice is used quite widely in the culture of various fruit and ornamental trees and shrubs. In

Fig. 85. Inarching, a type of grafting.

many cases, a bud on a plant will produce a twig which bears flowers or fruits different in some respect from the others on the same plant. An alteration of this kind in a twig is known as a **bud-sport,** or **mutation.** Bud-sports are commonly propagated by this method, in which a T-shaped slit is made in the bark of the stock, which must be young and slender, and a single bud from another plant is inserted in the slit in such a way that the flaps of the T close over its margins. The bud is then bound in place and grafting wax applied. Less common is **saddle-grafting,** in which the tip of

Fig. 86. Making a graft. A scion is being inserted into the stock in the cambial region of the latter.
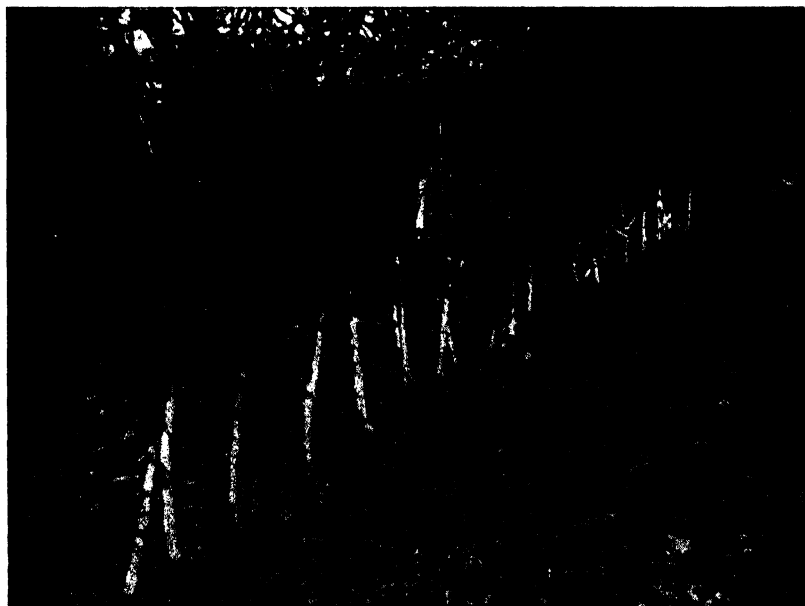
Fig. 87. Trees girdled by rabbits.

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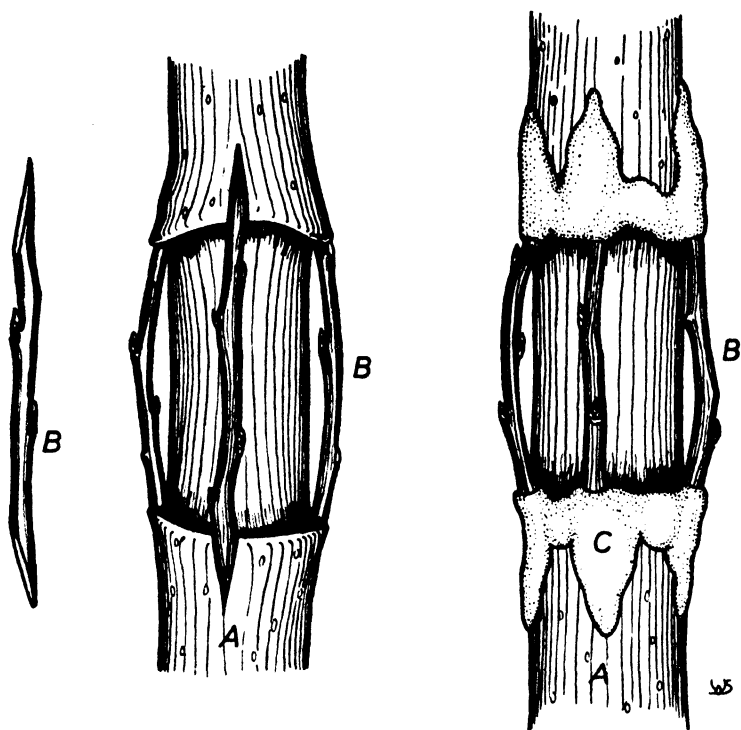
Fig. 88. Bridge-grafting

A. Stock.   B. Scions.   C. Grafting wax.

the stock is pointed and the base of the scion is notched to fit over the pointed stock. Another method of grafting, called **bridge-grafting,** is one which is employed to save trees which have been girdled by the gnawing of porcupines, rabbits (Figure 87), and other animals, or by insects or fungous diseases. Small branches are used as scions, the ends of which are inserted under the bark at the upper and lower borders of the girdle (Figure 88). If such a graft is successful, the phloem of the several small branches takes over the translocation functions of the destroyed tree bark, and the tree continues to live. These methods are illustrated in Figure 84.

Grafting is employed for several purposes, among which the following are common:

1. To propagate seedless varieties of plants, such as navel oranges.

2. To propagate without change, hybrid plants, the seeds of which do not all grow into plants like the parents (do not "come true").

3. To propagate plants, the seeds of which give low percentages of germination.

4. To increase the speed of propagation and induce more rapid fruiting. Many kinds of fruit trees bear fruit within a much shorter time if they are propagated by grafts, instead of by seeds.

5. To acclimate species of plants to strange environments. For example, cultivated apple varieties are frequently grafted on the stocks of Siberian crab apples, the roots of which are less susceptible to the rigors of Siberian winters than are the roots of the cultivated varieties. The roots of plum trees do not grow well in sandy soils, but plums can be successfully grown in such soils by grafting them onto the stocks of peach trees, the roots of which flourish in such soils.

6. To change or control the shape of a plant, as in the case of the umbrella catalpa, Camperdown elm, and others. The maximum stem circumference attained by almond trees is about five feet. If almond scions are grafted onto peach stocks, the trunks grow to circumferences of almost ten feet.

7. To check or eliminate parasites. In France and other parts of Europe, European types of grapes are seriously injured by a kind of root-louse which does not attack the roots of American grapes. In order to check this parasite, scions of European grapes are grafted onto American grape stocks. Thus, European grapes can be grown without damage by root-lice.

A common misconception concerning grafting is that it is a method of producing new types of plants. This error has arisen probably because of Burbank's work both with the creation of new varieties of plants and with propagation of plants by means of grafting. Grafting never results in the creation of new kinds of plants. It is exclusively a process of **vegetative** reproduction employed to achieve the continuance of varieties *without change*. New varieties arise naturally by **mutation** (a process of sudden unpredictable change) or they are isolated from other varieties by artificial selection or are developed by cross-breeding (**hybridizing**). After new varieties have developed, they are frequently propagated by grafting. Since many such varieties are hybrids, their seeds do not "breed true" — that is, all of them do not grow up into plants like their hybrid parent. In order to maintain and propagate such hybrid varieties, grafting or some other vegetative method of propagation is employed.

That grafting maintains the separate individualities of stock and scion has been shown by every successful graft. In some cases many
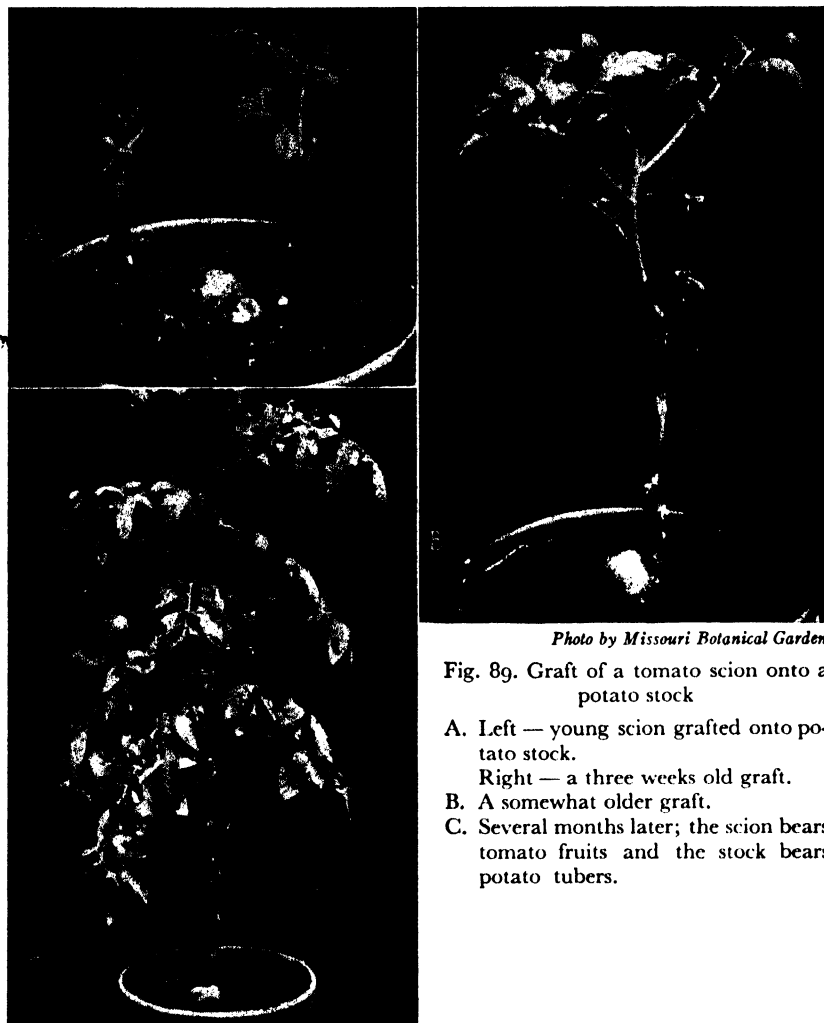
Photo by Missouri Botanical Garden

Fig. 89. Graft of a tomato scion onto a
            potato stock

A. Left — young scion grafted onto po-
   tato stock.
   Right — a three weeks old graft.
B. A somewhat older graft.
C. Several months later; the scion bears
   tomato fruits and the stock bears
   potato tubers.

closely-related varieties of scions may be grafted onto one stock, with
the result that separate branches of the grafted plant bear different
types of fruits or flowers. There are several well-known apple trees in
this country, for example, which have as many as 115 apple varieties
grafted to them. Each scion continues to produce apples of its variety,
with no mixture of the characteristics of the different varieties. Another
interesting type of graft can be made between scions of tomato ahd
stocks of potato (Figure 89); the stock continues to produce subter-

ranean tubers, the scion to form typical tomato fruits. Not only do the stock and scion in a graft-union retain their individual structural characteristics, but they also retain their characteristic physiological features. For example, when a sunflower scion is grafted onto a Jerusalem-artichoke stock, the sunflower portion of the graft stores a large part of its food as starch, while the tissues of the stock convert a large part of the food which passes down into them from the scion into inulin, a type of carbohydrate which is quite different from starch. In successful grafts, there is obviously an interchange of water, minerals, and organic materials between the tissues of the stock and

Photo by R. V. Drexler

Fig. 90. Natural graft between white ash trees.

those of the scion, and thus a stock may influence in some degree the rate of growth or some other physiological feature of a scion (and vice versa). Such mutual influences are usually rather minor, however, and in no case do they lead to the production of new kinds of plants — that is, they do not affect the hereditary potentialities of members of the graft.

Girdling is another horticulture practice, the success of which depends upon some knowledge of stem structure and functions. As stated earlier in this chapter, girdling is the removal of a complete ring of phloem down to the cambium or the wood from a branch or trunk of a woody plant. Girdling interrupts the downward passage of food through the phloem and thus causes food to accumulate above the girdle (Figures 91, 92). If a girdle is made on a small branch, just below flower or flower cluster, the fruits produced by the flowers will be unusually large because large amounts of downward-moving food which collects above the girdle pass into the developing fruits. This girdling of small branches is frequently employed in this country to produce

Photo by C. F. Hottes

Fig. 91. Girdling of a tree trunk by a rope.

Photo by C. F. Hottes

Fig. 92. Girdling of tree trunk by fence wire.

extra large grapes or other fruits chiefly for exhibition purposes. In Europe, girdling is practiced much more extensively than in this country for the production of oversize fruits which command high prices in European hotels and cafes. If, in the girdling of young branches, the cambium is not injured, the girdle is usually healed over by subsequent growth. If a complete girdle is cut through the bark and cambium of a tree trunk, the tree usually dies as a result of root starvation. Girdling of this type is frequently used to kill large numbers of trees preparatory to clearing forest areas for agricultural purposes.

The **injection** of chemicals into stems is another interesting application of a knowledge of stem structure and functions. In many types of soils, iron is not present in forms which can be readily utilized by green plants. The leaves of such plants growing in these soils fail to develop normal green color, because iron is required for the manufacture of chlorophyll. It has been found that the deposition or injection of water-soluble iron-salts into the sapwood of trees constitutes a simple remedy for this **chlorosis** and promotes the formation of normal quantities of chlorophyll. Poisons such as arsenic compounds and copper sulfate have been injected into sapwood to kill quickly trees on lands to be cleared for agricultural use and also to thin out dense forests. Several investigators have experimented upon the injection

into trees of chemicals poisonous to parasites in the hope of controlling in this manner the attacks of such organisms on trees. Lithium salts have been injected into chestnut trees in an effort to check the chestnut blight disease and enable the trees to form protective tissues to surround diseased portions of their stems. The injection of zinc chloride, copper sulfate, and other chemicals into the sapwood of trees has been reported to be moderately effective in reducing the depredations of certain kinds of bark-beetles. Research upon the use of such chemicals to kill or control fungi and insects in woody plants is not very far advanced and at this time the results of such investigation must be considered as inconclusive.

SUMMARY

1. The liquids which move upward or downward in stems are known as sap.

2. The conducting tissues of stems are xylem and phloem.

3. Xylem vessels and tracheids conduct water, mineral salts and sometimes foods, chiefly upward. Sieve tubes in the phloem conduct foods manufactured in the leaves chiefly downward. In many plants, there is also some upward conduction of mineral salts and foods in the phloem, especially in early spring in woody plants.

4. The term translocation is applied to the conduction of materials, especially foods, in plants.

5. The principal forces responsible for the rise of sap through xylem seem to be those which develop as a result of the evaporation of water from leaves, the imbibitional forces developed by partially dried leaf cells, the absorption of water from leaf veins by these cells as a result of their imbibitional forces, and the creation of a pull upon the water in the xylem tracheids and vessels. This pull is transmitted downward through stems and roots because of the tremendous cohesive powers of water molecules.

6. Other forces apparently of secondary importance in causing the ascent of sap are root pressure, the forces developed within living cells of the xylem, capillary forces in the walls of tracheids and vessels, and possibly others.

7. The forces responsible for the downward movement of foods in the phloem are inadequately known.

8. Pruning is a horticultural practice employed to control the shape of a woody plant or to remove dead or diseased limbs. In pruning, the limb which is to be removed should be cut away parallel to the main

branch from which it grows and as close to the main branch as possible to facilitate healing of the wound. Pruning is also employed to control flowering.

9. Girdling is the removal of a complete ring of bark to the cambium or wood. The girdling of small branches of woody plants is employed to produce unusually large fruits or to force limbs into flowering. A girdle on a tree trunk interrupts the passage of food downward through the phloem and results in the starvation and death of the roots and thus of the whole tree.

10. Grafting is the uniting of a twig (scion) of one plant upon the stump (stock) of another. The tissues of stock and scion grow together in a successful graft. Grafting is a means of vegetative propagation and does not bring about the development of new types of plants.

11. Grafting is employed to:

    a. Propagate seedless varieties of plants.

    b. Propagate plants with seeds of poor germinating power.

    c. To combat certain plant diseases.

    d. To acclimate plants to new regions and adjust them to different climatic factors.

    e. To decrease the time required for flowering and fruiting.

    f. To change or control the shape of a plant.

    g. To propagate hybrid plants, the seeds of which do not come true.

The Structure and Economic Importance of Leaves

LEAVES ARE the food-making organs of plants and thus are vitally important to plants themselves and likewise to all members of the animal kingdom. All foods used by living organisms of all kinds (except a few species of bacteria) are direct or indirect products of green leaves. **Herbivorous** (plant-eating) animals, most fungi, and other organisms incapable of making their own food obtain their nourishment directly from leaves or other parts of plant bodies, living or dead; **carnivorous** (meat-eating) animals and certain species of fungi derive their food from the tissues of living animals, which in turn eat smaller animals or green plants.

1. THE NATURE, ORIGIN, AND ARRANGEMENT OF LEAVES

Leaves are the most characteristic appendages of aerial stems. They vary enormously in their forms, sizes, and internal structure in different species of plants and to some degree in the same plant. In most kinds of plants, leaves are expanded and flattened in form, though occasionally they are needle- or scale-like, as in pines and junipers, nearly cylindrical, as in onions, or of some other shape. There are some types of leaves which are so specialized in structure in the performance of functions other than food manufacture, that they are scarcely recognizable as leaves. Leaves of this type will be described later in this chapter. Leaves arise from stems at nodes and almost invariably have buds in their axils. As stated in an earlier chapter, leaves originate as lateral protuberances of the apical meristems in buds. With the opening of a bud, these leaf primordia begin to grow rapidly in size as a result of cell division, enlargement, and differentiation until they reach the full size of mature leaves.

Fig. 93. Leaf arrangement
A. Alternate leaves of elm.
B. Opposite leaves of a mint (*Scutellaria*).
C. Whorled leaves of Culver's-root (*Veronica*).

Leaves are arranged on stems in the same manner as buds (Figure 93). Leaves are most commonly **alternate** (Figure 94), or **spiral** in their arrangement, as in elms, lindens, and apples. In this distribution there is only one leaf at a node. Less common is the **opposite** (Figure 95) arrangement, in which two leaves occur at a node, usually on opposite sides of the stem, as in maples, buckeyes, carnations, and dogwoods. In the **whorled** distribution, there are three or more leaves at a node, more or less equally spaced around the node; this arrangement occurs in catalpas, in bed-straw, and in certain species of lilies. In the various dispositions of leaves on stems, it is apparent that the arrangement of leaves is such that the weight of the leaves is more or less equally distributed on all sides of the stem and that there is a minimum degree of mutual shading.

2. EXTERNAL STRUCTURE OF FOLIAGE LEAVES

The green, food-making leaves of plants are termed **foliage** leaves. A typical foliage leaf consists of a leaf stalk, or **petiole**, a usually-flattened, expanded portion at the end of the petiole, the **blade** and in some species of plants, such as roses, small green appendages, termed

Fig. 94. Alternate leaves of black-gum (*Nyssa sylvatica*).

Fig. 95. Opposite leaves of privet.

stipules at the points of juncture of petioles with stems. Stipules are absent from the leaves of many plants and in others fall off shortly after the buds open. Stipules are apparently not of fundamental importance in the physiology of most plants. However, in some species such as the tulip tree, they furnish protection for developing buds in leaf axils (Figure 100). In Japanese quince and in the garden pea the stipules are commonly 1 inch or more wide, and, since they are green, manufacture food. Some leaves lack petioles, their blades growing directly from the stem, a condition described as **sessile.** Petioles are generally slender and cylindrical in form, but in some plants, such as grasses and bananas, they may be flattened into **sheaths** which clasp the stem. Petioles conduct water and solutes from the stems into leaf blades and transport foods manufactured in the blades downward into the stem. As a result of the ability of petioles to bend, they move the blades which they support into positions in which the maximum areas of the blade surface are exposed directly to light, which is necessary for food manufacture. Sometimes the bases of petioles are swollen in such a manner as to form a protective cap over young axillary buds, as in sycamore trees.

Leaf blades are in most plants flat, thin, and broad, with a con-
spicuous system of **veins** forming the structural framework of the blades.
These veins branch from the apex of the petiole at the base of the blade
and they are composed of xylem and phloem cells continuous with
those of the petiole. Thus, in addition to forming the structural frame-
work of blades, veins are the ultimate branches of the conducting
channels which pass into leaves from the conducting tissues of stems.
The arrangement of veins (**venation**) varies in the leaves of different
species of plants, but usually conforms to one of two types: **parallel**
and **netted**. In leaves with parallel venation, such as those of iris,
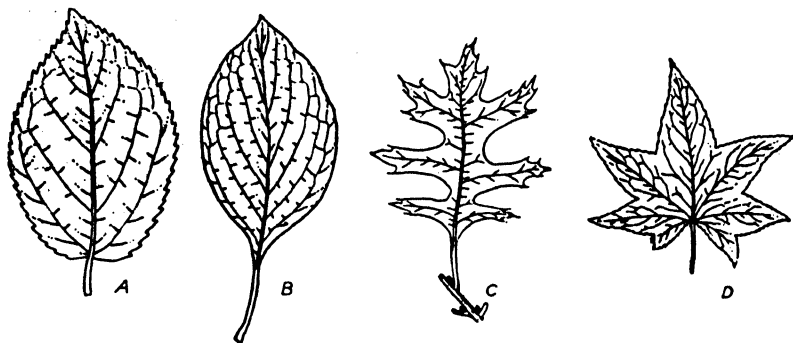
Fig. 96. Dicot leaves, with netted-venation

A. Toothed leaf.   C. Pinnately lobed leaf.
B. Entire-margined leaf.   D. Palmately lobed leaf.

lilies, and corn, wheat, and other grasses, the main veins are parallel
with each other and are arranged lengthwise (Figure 98). In leaves with
netted-venation, such as those of maples, linden, geranium, and sun-
flowers, the veins branch profusely in such a manner that they are not
parallel to each other, but form a network. There are many variations
in these arrangements. In cannas and bananas, for example, the vena-
tion is said to be **pinnately parallel**; there is only one longitudinal vein,
a central midrib from which a number of smaller veins branch out at
the same angle toward the margins, in the same fashion as the barbs
of a feather extend outward from the central rib of the feather. In some
leaves with netted-venation, such as those of elm and oak, there is one
main vein, which is an extension of the petiole; from this main vein the
branch veins arise, such as in banana and canna leaves, except that
they are not parallel to each other. A net-system of this type is termed
pinnate venation. In leaves with **palmate venation**, such as those of
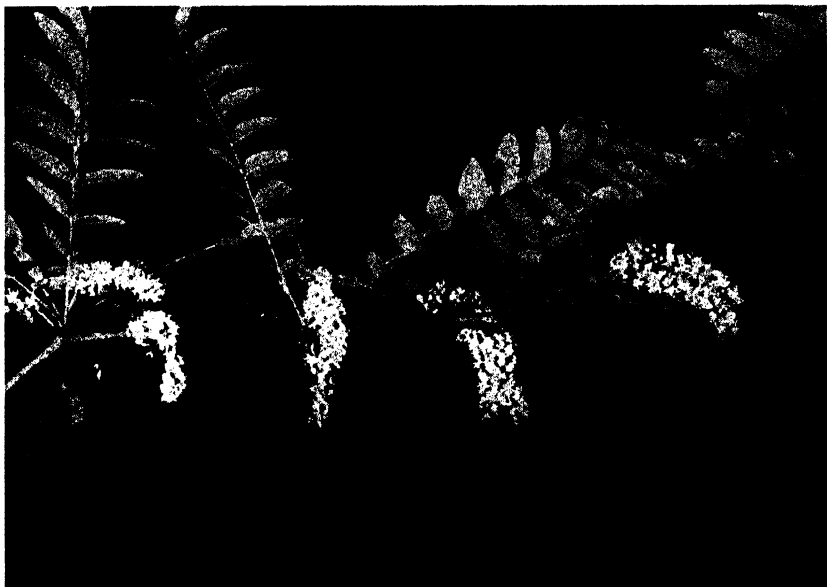
Fig. 97. Pinnately compound leaves of honey locust tree.

Fig. 98. Parallel-veined leaves of *Pitcairnia*, a monocotyledonous plant.
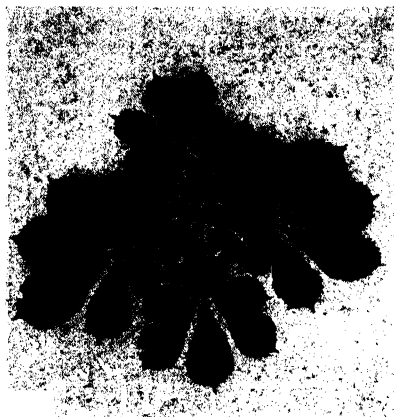
Photo by C. F. Holtes

Fig. 99. Palmately compound leaves of horse-chestnut (*Aesculus hippocastanum*).

sycamore, cucumber, and maple, there are several main veins which branch into the leaf blade at the tip of the petiole. Parallel-veined leaves are found in most monocotyledons, net-veined leaves in dicotyledons.

Leaf blades vary greatly in the degree of their division, their margins, their form, and their size (Figure 96). In some plants, for example, locusts, clovers, roses, and walnuts, the leaf blade is not in one piece, but is divided into a number of separate segments. A leaf of this type is termed **compound** and the individual segments of the blade are called **leaflets**. In **pinnately compound** leaves (Figure 97), such as those of walnut and rose, the leaflets are spaced along a somewhat elongated petiole. In the **palmately compound** leaves (Figure 99) of buckeye and clover, the leaflets are all attached at the tip of a petiole, not spaced along it as in walnut and rose leaves. More common than compound leaves are **simple** leaves, those in which the blade consists of a single piece, as in elm, peach, maple, and oak leaves.

The blades of leaves differ also in their margins. The leaves of irises, corn, lilies, dogwood, nasturtium, and privet have **entire** margins, that is, smooth margins which lack indentations. In **toothed** and **wave-margined** leaves, the margins are respectively indented by small to moderate-sized teeth, like those of a saw, and by small undulations or rounded teeth. The leaves of elm, cherry, and linden are toothed, those of chestnut are wave-margined. **Lobed** leaves are those in which the marginal indentations are much deeper than those between the teeth of toothed leaves. In lobed leaves, these indentations frequently extend inward almost to the main veins. **Pinnately lobed** leaves are those in which the indentations extend toward the midrib, following the pinnate venation of such leaves, as in red oak and bur oak. In **palmately lobed** leaves, such as those of sycamore and maples, the indentations extend toward the base of the leaf, in accordance with the palmate venation of these leaves. These marginal differences are shown in Figure 96.
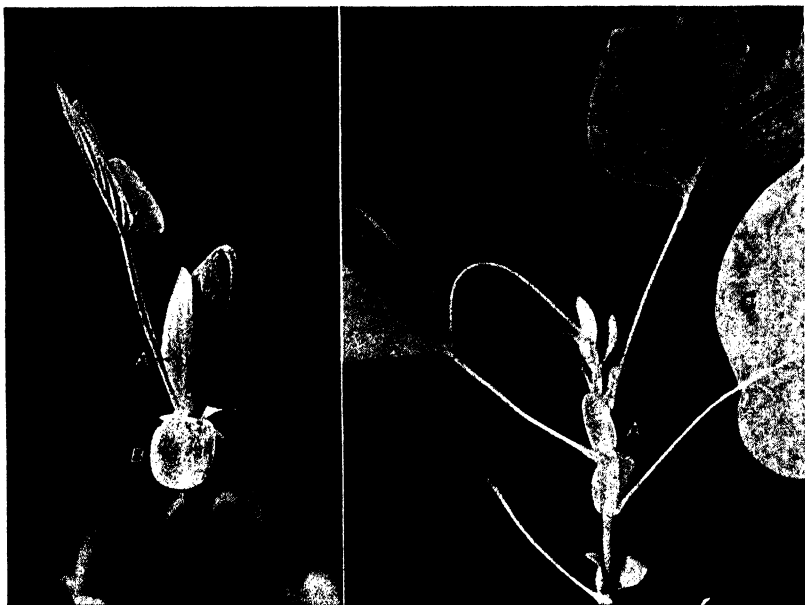
Fig. 100. Twigs of tulip tree

A. Stipules.   B. Bud scales.   C. Leaves.

The form of leaf blades varies from **linear**, as in blue-grass and wheat, to **circular**, as in nasturtium, with many intergrading forms, such as **lanceolate** (willows), **heart-shaped** (linden), **ovate** (hackberry), and many others. Leaves also differ greatly in size, from leaves a fraction of an inch in length and width, such as those of cedars, to leaves 12 to 15 or more feet long and one to two feet or more wide, such as those of certain palm trees and banana plants. These various characters of leaves — size, degree of division of the blade, nature of leaf margins, and blade form — are important in identifying plants and as such are tools with which students must be acquainted, if they are to learn to distinguish successfully among plant species.

A point which deserves emphasis is this: of the many variations in leaf form, marginal indentation, etc., there is apparently no single pattern which renders a certain type of leaf more successful than the many other kinds found in other species of plants. The very fact that there exists such diversity in the external morphology of leaves attests to the fact that there seems to be little functional significance in such diversity and that all foliage leaves, regardless of whether they are

toothed or lobed, simple or compound, so long as they are well provided with chlorophyll, are efficient food-making machines.

3. THE INTERNAL STRUCTURE OF LEAVES

A microscopic examination of a transverse section of a leaf shows three groups of tissues: **epidermis, mesophyll,** and **veins** (Figures 101, 102). The epidermis is a single layer of cells forming a surface skin which covers the entire leaf surface. Its chief function is the protection of the internal tissues of leaves from excessive loss of moisture. In some leaves it also furnishes a degree of protection against mechanical injury and also against the entry of parasites. The outer walls of epidermal cells are frequently thickened and are usually covered with a layer of **cutin,** a waxy material which is secreted on the outer surface of the cell walls by the protoplasts of the epidermal cells and which is in large part responsible for the protective efficiency of the epidermis. Epidermal cells are generally colorless, though in some plants, such as Wandering Jew and *Coleus,* purple or reddish pigments may be dissolved in the cell sap of the epidermal cells. Certain cells of the epidermis contain chloroplasts. These cells, which are termed **guard cells,** are somewhat bean-shaped, as seen in surface view, and are arranged in pairs, more or less regularly distributed among the more numerous, colorless cells of the epidermis, chiefly on the lower surfaces of leaves (Figure 104). Each pair of guard cells encloses a small pore, or **stoma** (Figure 103), through which gaseous exchange between the inside of the leaf and the external atmosphere and water evaporation occurs. These paired guard cells expand and contract with changes in their water content and as they do so, the size of the stoma which they enclose changes. When the guard cells are expanded, the stomata are open; when their water content decreases and they contract, the stomata are nearly or completely closed. The stomatal numbers of several species of plants are shown in the table below. Remember that

	Number of stomata per sq. mm. of leaf surface		Total number of stomata on lower surfaces of a leaf
	Upper surface	Lower surface	
Sunflower	175	325	1,950,000
Cottonwood	89	132	1,048,000
Olive	0	625	500,000˙
Birch	0	237	825,000
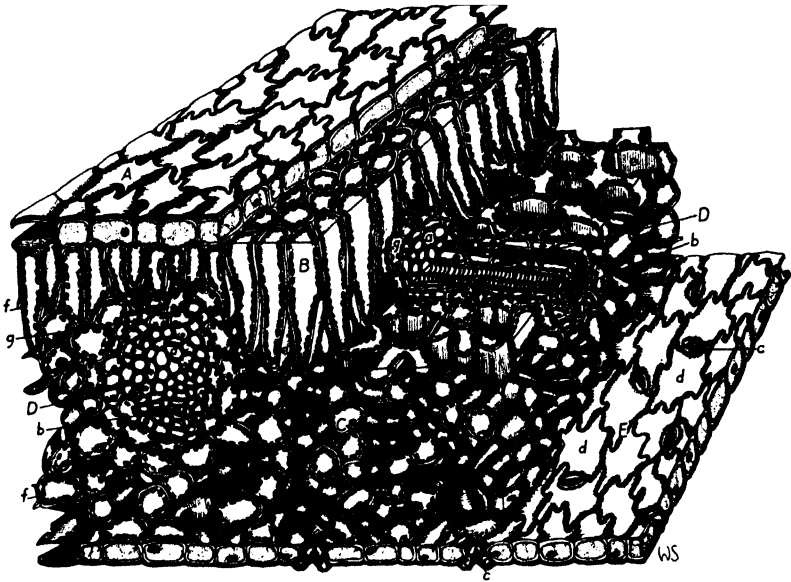
Fig. 101. Three-dimensional view of a dissected leaf

A. Upper epidermis.   B. Palisade tissue.   C. Spongy tissue.
D. Vein: a. xylem, b. phloem, g. bundle sheath.
E. Lower epidermis: c. guard cells with enclosed stoma, d. ordinary epidermal
cells, e. intercellular spaces, f. chloroplasts.

Fig. 102. Photomicrograph of a cross-section of a lilac leaf. Note the large vein in
section.

a square millimeter is approximately one square twenty-fifth of an inch. The average areas of most stomata when fully opened are between .000092 and .000100 square millimeters. The enormous numbers of stomata in the leaves of these plants are apparent in the table.

In many plants, **hairs** occur as outgrowths of leaf epidermal cells, as in heliotropes. They consist of small filaments of cells arranged end to end, as in cucumbers, or they may be formed of branched filaments, as in sycamore leaves. In some plants, geraniums and petunias, for example, the terminal cells of such hairs are glandular and secrete sticky materials which give the leaves a clammy texture. In other species, the epidermal hairs soon die and become dry and grayish or white in color.

The upper and lower epidermal layers of leaves are usually much alike in their detailed structure, except that in most species of plants, the cutin layer (**cuticle**) is thicker on the upper epidermis than it is on the lower and stomata are more abundant in the lower epidermis. In some cases, as in olive leaves, there are no stomata whatever on the upper epidermis. The thicker cuticle and smaller number of stomata in the upper epidermis constitute an advantageous arrangement, for the upper surfaces of leaves are more directly exposed to the drying action of the sun's rays than are the lower epidermal cells.

Fig. 103. Portion of leaf epidermis

A. Guard cells: a. cell wall, b. nucleus, c. chloroplast.
B. Stoma.
C. Ordinary epidermal cells.

The mesophyll tissues consist of thin-walled, parenchyma cells which contain numerous chloroplasts. These are the food-making cells of leaves. The mesophyll cells nearest the upper epidermis are closely packed cylindrical cells which are arranged at right angles to the leaf surface. These constitute the **palisade** layer of the mesophyll. In the leaves of most plants, there are one or two such palisade layers just beneath the upper epidermis. Below the palisade cells is a second group of parenchyma cells of different form and arrangement. These cells are usually quite variable in shape and are loosely packed in such a manner that there are numerous air spaces among them. These cells
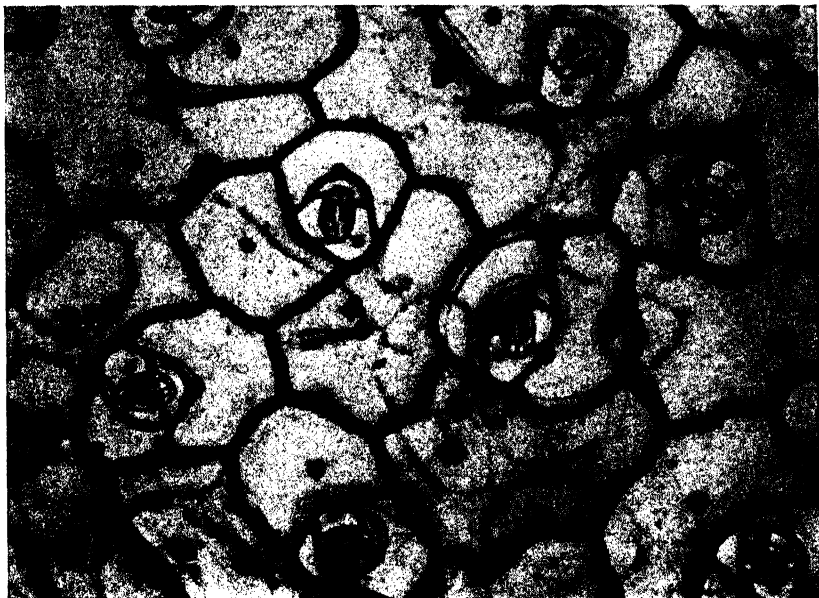
Fig. 104. Epidermis of *Sedum*, showing guard cells and stomata.

constitute the **spongy** layer of the mesophyll. Like the palisade cells, the cells of the spongy layer contain numerous chloroplasts and thus are food-making cells. The numerous air spaces facilitate the diffusion of gases through the internal portions of leaves for they connect with the spaces underlying the stomata. The type of mesophyll differentiation which has just been described is characteristic of most leaves which grow in a horizontal or oblique position. In certain grasses, irises and other species in which the leaves stand in a more or less vertical position, there are palisade layers under both epidermal layers with the spongy tissue between them. The former arrangement of tissues is by far the more common.

The veins are vascular bundles which branch out from the vascular bundles of the petiole at the apices of petioles into the blades of leaves, as described earlier in this chapter. These veins extend through the mesophyll tissues, surrounded by the cells of the latter. The main veins frequently appear in relief on the lower surfaces of leaves and as shallow depressions on the upper surfaces. Each vein is made up of both xylem (vessels and tracheids) and phloem (sieve tubes, chiefly), which conduct respectively water and minerals upward into leaf blades and

Fig. 105. Plant of *Mesembryanthemum tigrinum*, showing water-storage leaves.

foods manufactured in the leaves downward into the petiole for transfer to the stems and roots. In the leaves of most plants, the xylem cells form the upper portions of the veins, the phloem cells the lower portions. Each vein is surrounded by a group of cells, known as a **bundle-sheath**, which gives support to the vein and aids in the conduction of substances. In the bundle-sheaths of the larger veins, thick-walled strengthening cells are usually present. The degree of branching of the leaf veins is such that no mesophyll cell of a leaf is far removed from the terminus of a veinlet. It has been estimated that there may be as many as 25,000 of these veinlet endings in one square inch of leaf surface.

4. SPECIALIZED LEAVES

There are several kinds of leaves which perform functions other than that of food manufacture and which possess corresponding structural peculiarities reflecting these specialized functions. Of most common occurrence among the various kinds of specialized leaves are the protective **bud-scales** of woody plants, described in an earlier chapter. In barberry, certain species of cacti, and other species, the **spines** are morphologically specialized leaves, for they bear buds in their axils. These spines are doubtless of some value in discouraging the visits of

grazing animals. In the black-locust, the spines which occur in pairs at the points of juncture of petioles and stems are modified stipules. In onion and lily bulbs, the **bulb-scales** are leaves specialized for the storage of food. The leaves of *Sedum*, of *Portulaca* (flowering "moss"), of various other members of the live-for-ever family and of century plants, are very thick and succulent because of the large quantities of water which they store in their cells (Figure 105). These leaves frequently contain sticky, gummy colloidal materials which hold water very tenaciously against the drying forces of the arid or semi-arid regions in which these plants usually grow. The leaves of some plants function wholly, or in part, as **tendrils** (Figure 106), structures which twine about solid objects and thus aid in supporting the plants which bear them. In peas, some of the leaflets of the compound leaves are slender tendrils, instead of flat, broad leaflets. Nasturtium plants have no specialized tendrils, but their petioles twine around suitable supports. Among the leaves of
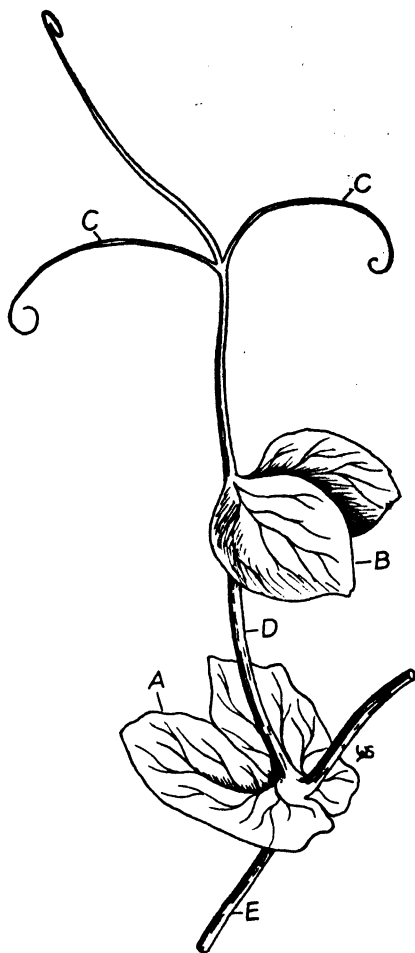
Fig. 106. Compound leaf of pea

A. Stipule.   D. Petiole.
B. Normal leaflet.   E. Stem.
C. Tendril.

seed plants there are some which provide for **vegetative reproduction,** as well as food manufacture. In *Bryophyllum*, for example, the leaves produce new plants at their notches (Figure 107). These plants become loosened and may fall to the ground; if their roots reach moist soil, these plantlets grow into new plants.

Doubtless the most highly specialized and most amazing of all the kinds of modified leaves are the **insectivorous** or **carnivorous** leaves of

Fig. 107. Development of plantlets in
leaf notches of air-plant (*Bryophyllum*).

Fig. 108. A tropical pitcher plant
(*Nepenthes Curtisii*).

Fig. 109. A tropical pitcher plant
(*Nepenthes dominii*).
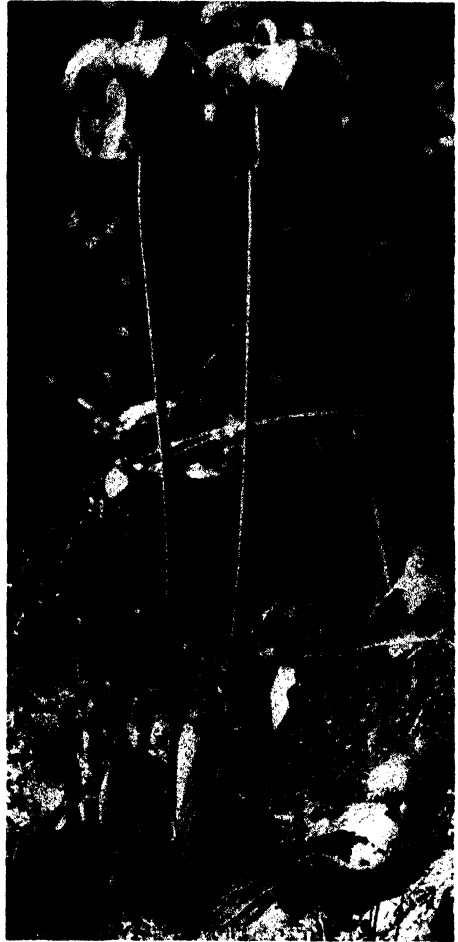
Fig. 110. A pitcher plant (*Sarra-cenia*) in flower. Note the pitcher-shaped leaves. Northeastern United States.

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almost 200 species of angiosperms. These plants grow principally in bogs, the soil of which is deficient in certain essential elements, or which contains these elements in forms not readily available to green plants. Insectivorous plants secure certain of these elements by trapping and digesting the bodies of insects and other small animals. These plants are chlorophyllous and make their own food; their use of animal tissues as a source of food is supplementary to their own food-making and they are able to develop in apparently normal fashion without digesting insects, if their roots obtain the required mineral nutrients.

The pitcher plants, of which there are both tropical and temperate
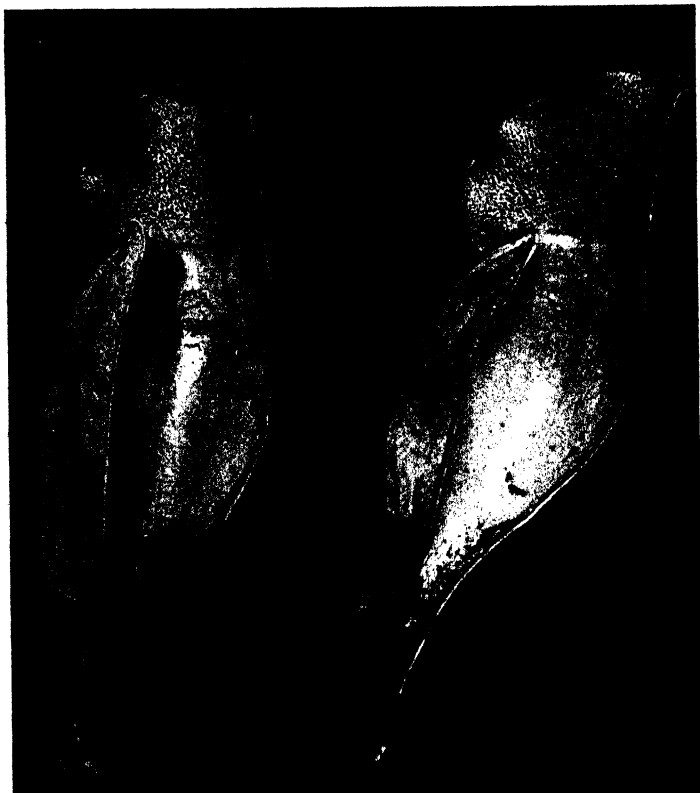
Photo by C. F. Hottes

Fig. 111. Sectioned leaves of *Sarracenia*, showing bristles.

zone species, have leaves which are tubular or pitcher-shaped, and which hold a liquid containing digestive substances (enzymes). Insects attracted to the pitchers by their colors or odors crawl into them over a number of stiff, downward-pointing hairs inside the pitcher. When they attempt to crawl out, they are frequently unable to climb upward over the bristly hairs and after becoming exhausted fall into the liquid and are drowned, following which the soft portions of their bodies are digested and absorbed by the leaf cells. Some of the Malayan species (Figures 108, 109) have leaf-pitchers which are 18 inches long and which hold as much as a quart of liquid. There are pitcher plants in the United States, of which the *Sarracenias* (Figures 110, 111) occur in bogs in many parts of the Middle Western and Eastern states. In one species of *Sarracenia* the leaves are occasionally a yard long.

Fig. 112. Western pitcher plant (*Darlingtonia*), from Oregon.
Photo by C. F. Holtes

The sundews constitute another interesting group of insectivorous plants. In these, the leaf blades are circular and flattened, and possess numerous glandular hairs which grow vertically and obliquely upward from the upper surfaces of the leaves. These tentacles, about 150 to 200 per leaf, secrete sticky substances containing digestive juices. When an insect alights on one of these leaves it is smeared by the mucilaginous secretions of the glands at the tentacle tips. Simultaneously some of the tentacles, which are sensitive to contacts of as little as .000822 milligrams (.000000028770 oz.), bend inward and surround the body of the insect. The movement of these tentacles is frequently very rapid, in some cases requiring only 4 or 5 minutes for completion. The fluid with which the bodies of insects are covered contains digestive agents which convert the nitrogenous substances of the insects into forms which the leaves can utilize (Figures 114, 115).

The Venus'-flytrap has leaf blades along the margins of which are from 12 to 20 bristly teeth, frequently one-half inch long. On the inner (upper) surface of the blade are several slender hairs which are sensi-
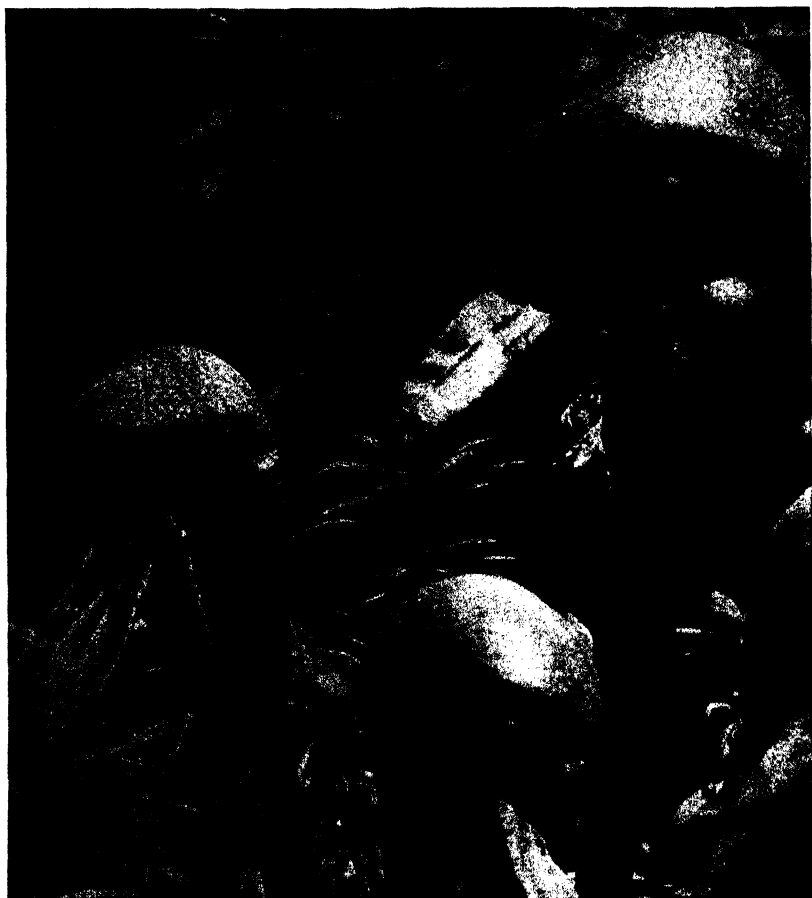
Fig. 113. Leaves of *Darlingtonia*, showing openings on underside of crook.

tive to contact. If an insect on the leaf touches the sensitive hairs, a stimulation is initiated which causes the two halves of the leaf to move together, in the same manner as a book is closed. The marginal bristles interlock and the insect is securely held within the trap. Glands on the inner surface of the leaf then digest the body of the entrapped insect. After the complete digestion of the soft parts of the insect's body, the leaf opens again. The time required for the closing of the leaf-halves following stimulation is very short, frequently as brief as 8–10 seconds if the atmosphere is warm and humid.

In bladderworts, aquatic plants found in many lakes and ponds,

Fig. 114. Plants of sun-
dew (*Drosera rotundifolia*).
The circle in the lower
right corner is the rim of a
half-dollar.

Photo by C. F. Hottes
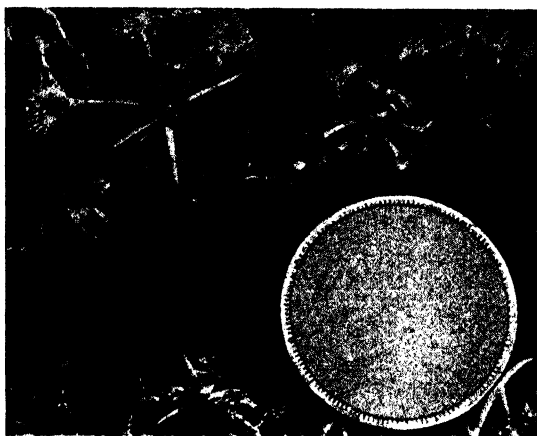
there are numerous tiny bladders, borne on the submerged stems.
Each bladder has a trap-door-like valve which opens only inward, not
outward. When water animals, such as tiny crustaceans, larvae of
gnats, and other small insects, come in contact with these bladders, the
largest of which are about 6 mm. in diameter, they are drawn into
the bladders through the one-way trap-doors when negative pressures
exist inside, and are unable to escape. Within a few hours the digestion
of the bodies of these animals begins.

In many other species of insectivorous plants, there are no highly
specialized leaves of the type described above. In such species, the sur-
faces of the leaves are covered with sticky, glandular hairs, upon which
insects become glued. Some of these glands secrete juices which digest
the bodies of captured insects. One of the species of this type is used by
people in the rural districts of Portugal as a substitute for fly-paper.
The plants are hung in doorways and by means of their sticky leaf
secretions firmly hold insects which alight upon them.

There are many superstitions about these insectivorous plants, chief
of which is that there exist plants able to entrap and digest the bodies
of large mammals, including man. Occasionally stories of this nature
find their way into the columns of tabloids, but they have never been
authenticated by reputable scientists. The known carnivorous plants
limit their captures to small insects, crustaceans, and other small water
animals. There are cases known in which small frogs have fallen into
leaf-pitchers and have been partially digested. The leaves of many
insectivorous plants are able to digest proteinaceous materials given to
them artificially; such foods as meat and hard-boiled eggs are partially
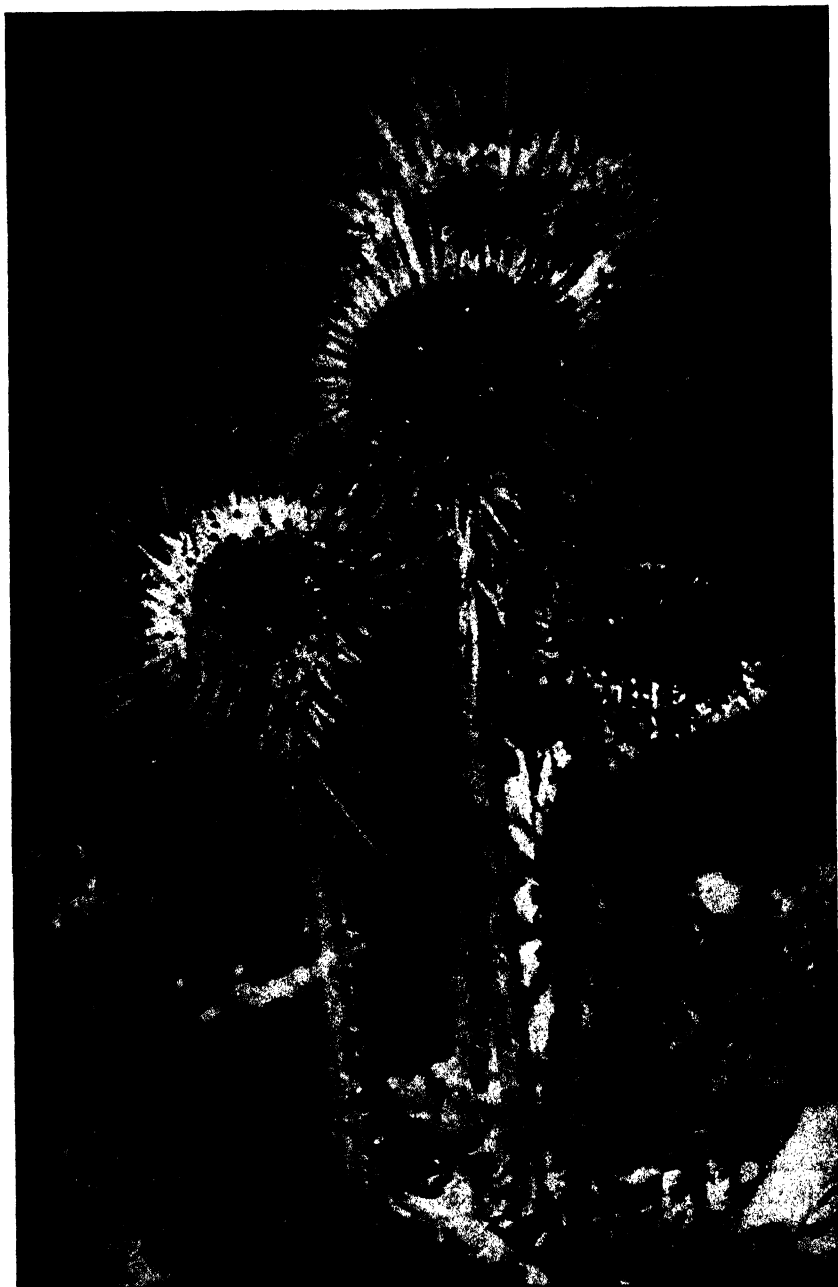
Fig. 115. Leaves of sundew (*Drosera rotundifolia*).
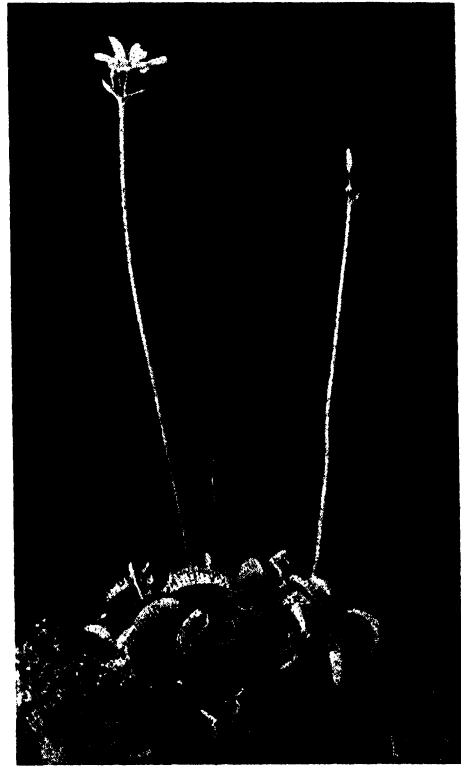
Fig. 116. Plants of Venus'-flytrap
(*Dionaea*).
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or wholly digested, for example, by the leaves of Venus'-flytrap and of certain species of pitcher plants.

5. ECONOMIC IMPORTANCE OF LEAVES

The fundamental importance of leaves to man rests upon their ability to make foods and vitamins which he can utilize as sources of nutriment for himself and for his domesticated animals. Of the many kinds of plants which furnish food for cattle, sheep and horses, most valuable are the grasses, which form dense mats of leafy vegetation over vast stretches of the plains regions of the world. Important plants, the leaves of which are used directly by man as a source of food, are artichoke, cabbage, collards, Brussels sprouts, broccoli, celery, endive, lettuce, rhubarb, spinach, Chinese cabbage and water cress. Economically important products other than foods are derived from the leaves of many of the plants. Among such materials are tannins
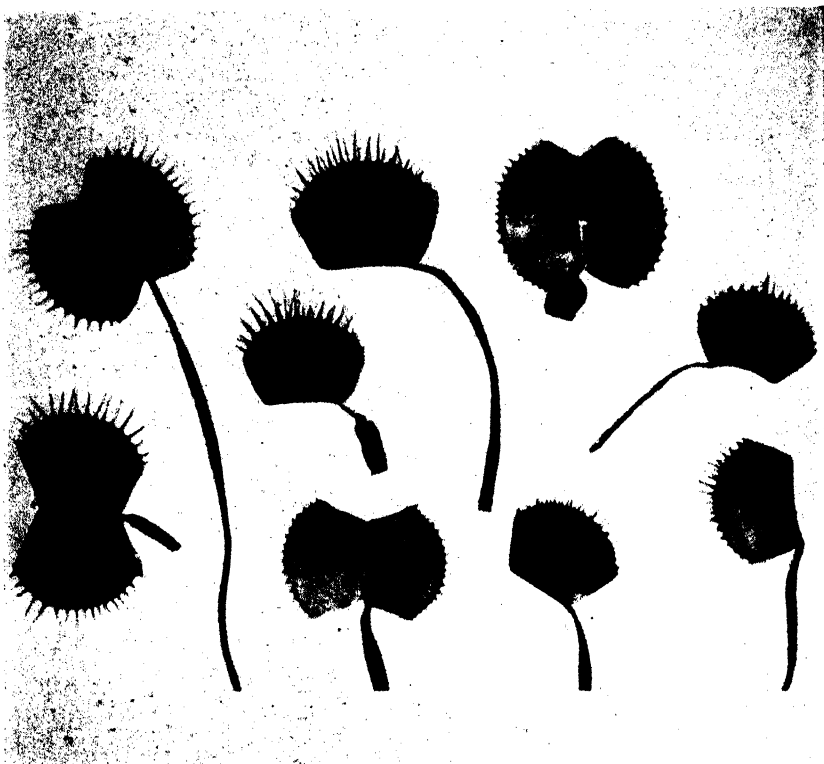
Fig. 117. Leaves of Venus'-flytrap (*Dionaea*).

(from sumac leaves), dyes (indigo and henna), aromatic oils for per-fumes, soaps, spices and flavoring extracts (geranium, citronella, bay, marjoram, peppermint, sage, spearmint, thyme, parsley, wintergreen, and tansy), drugs (belladonna, cocaine, digitalis, eucalyptus, witch hazel, hoarhound, senna, and pennyroyal), tobacco, tea, and chloro-phyll, used as a dye in soaps, candles, foods, and oils.

SUMMARY

1. The chief function of leaves is food manufacture.
2. Leaves are usually flattened, expanded structures, although some-times they are needle- or scale-like.
3. Leaves develop as lateral protuberances of the growing points of buds.

1.   2.

3.   4.

5.   6.
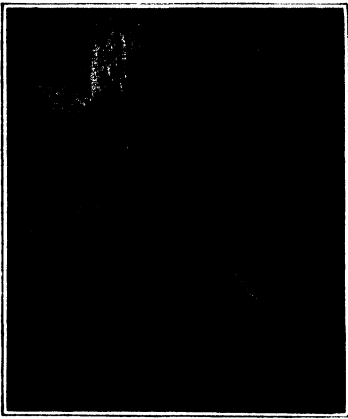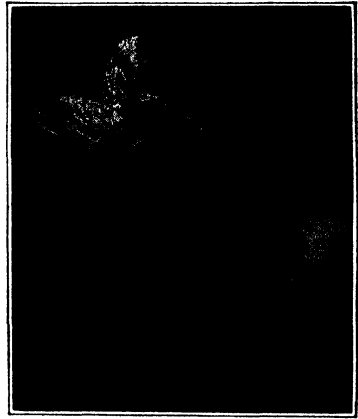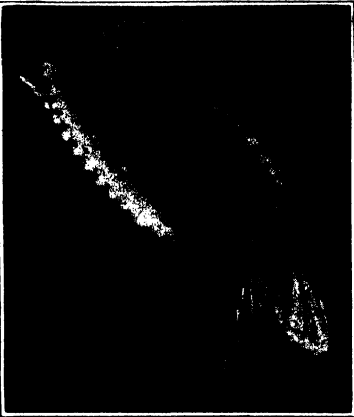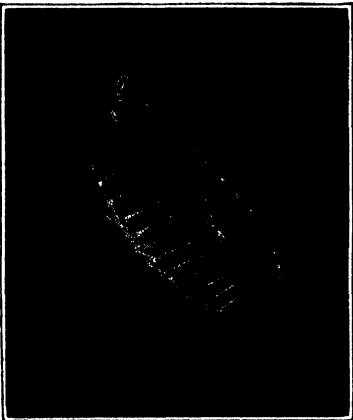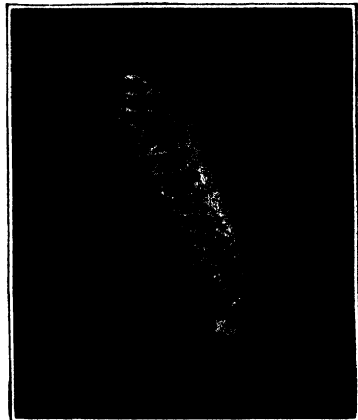
Fig. 117a. Stages in the capture of a fly by a leaf of Venus'-flytrap.

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4. Leaves are arranged in the same manner as buds. These arrangements are spiral (alternate), opposite and whorled. Buds develop in the axils of leaves.

5. A typical foliage leaf consists of:
   a. a stalk (petiole).
   b. an expanded portion (blade).
   c. often a pair of stipules at the base of the petiole.

6. Leaves vary greatly in their sizes, forms, margins, venations, and degree of division of their blades.

7. Parallel-veined leaves are characteristic of most monocots, netted-veined leaves of most dicots.

8. The surface layer of cells of leaves is the epidermis.

9. Between the upper and lower epidermal layers are the mesophyll tissues. These consist typically of vertically elongated cylindrical palisade cells, situated usually in one or two layers just beneath the upper epidermis, and a spongy layer, located below the palisade cells. The spongy tissue consists of loosely-packed, rather irregular cells with numerous intercellular spaces. Extending through the mesophyll tissues are the veins which branch out from the petiole or its continuation in the blade, the midrib.

10. Epidermal cells usually have cutinized outer walls and serve principally in protecting the mesophyll against excessive drying. Occurring in pairs in the epidermis are green guard cells, each pair enclosing a leaf-pore, or stoma.

11. The mesophyll cells are rich in chlorophyll and constitute the chief food-making cells of leaves.

12. The xylem cells of veins conduct water and minerals into leaves and the phloem cells of veins conduct foods downward into the stems.

13. Examples of structurally and functionally specialized leaves are:
   a. bud scales.
   b. certain types of spines.
   c. bulb-scales.
   d. tendrils.
   e. insectivorous leaves.
   f. storage leaves.

The Physiology of Leaves

1. LEAF–FALL

THE LEAVES of **deciduous** trees and shrubs fall off the branches from which they grow at the end of their growing season, as contrasted with those of **evergreens,** in which the leaves persist for several seasons, often as long as four years. Evergreens do not retain the same leaves always, but shed them at intervals, usually as new leaves are formed. The causes of leaf-fall are similar in both deciduous trees and evergreens; the difference between these types of woody plants thus lies in the time and the extent of their leaf-shedding. The causes of leaf-fall are worthy of consideration as among the most interesting physiological activities which occur within leaves. In autumn, certain cells at the base of the petiole become meristematic and form a layer of thin-walled cells across the petiole base. This layer, known as the **abscission layer,** begins to disintegrate shortly after its formation, as a result of the softening of its cell walls. This disintegration continues until the leaf is held to the stem merely by the vascular bundles of the petiole. With the repeated swaying caused by winds and also as a result of frost action, the abscission layer ruptures and, following its disintegration, there develops just below it at the very base of the petiole a layer of cork cells which form a protective covering over the leaf scar.

In some deciduous trees, such as red oaks, a large number of dead leaves remains on the branches throughout the winter. This persistence of dead leaves is attributable usually to the lack of an abscission layer and to the failure of the tough vascular bundles of the petiole to break.

2. THE COLORS OF LEAVES

The predominating color of foliage leaves is green and is caused by the presence of the green pigment **chlorophyll** which constitutes the fundamental machinery of food manufacture in plants. Chlorophyll is

actually made up of two closely related pigments called **chlorophyll A** and **chlorophyll B,** but for the sake of convenience they are commonly referred to by the single name *chlorophyll*. Chlorophyll is an unstable pigment and is continually being decomposed by light. Simultaneously it is synthesized by the living cells of leaves, so that the chlorophyll content of leaves does not alter appreciably during the growing season. Though strong light has a destructive effect upon chlorophyll, it is a necessary factor for chlorophyll synthesis, as is shown by the fact that plants kept in darkness do not become green. Along with chlorophyll there are present in most leaves two other pigments, yellowish **xanthophyll** and yellowish-orange **carotin.** These substances are present in relatively small quantities as compared with chlorophyll and hence their colors are usually masked by the green of chlorophyll. In some leaves with larger amounts of these yellow pigments, the deep green color of chlorophyll is somewhat lightened by the color of the carotin and xanthophyll. The exact function of these yellow pigments is not known, but there is evidence which points to a definite connection between carotin and vitamin A production, at least in animal tissues. The exact functions of vitamin A and other vitamins in plants are not known with certainty.

The above-mentioned pigments occur mainly in plastids, rarely dissolved in cell sap. They are frequently found, as indicated in earlier chapters, in organs other than leaves; they often occur in herbaceous and young woody stems and occasionally in roots.

The reddish-blue and purple colors of various plant parts are attributable principally to a class of pigments known as **anthocyanins.** These pigments are always found dissolved in cell sap and are never present in plastids, as are chlorophyll, xanthophyll, and carotin. The anthocyanins occur commonly in the petals of red, blue, purple, and lavender flowers and are also frequently present in leaves (Wandering Jew, purple cabbage), roots (garden beet), fruits (grapes), and occasionally stems, usually in the epidermal cells of the organs. Whether these pigments have any direct significance in the physiology of plants is not known. The abundance of such colored compounds in flowers indicates they are probably important in attracting insects, which are necessary for the pollination of most kinds of flowers. Some botanists believe that anthocyanins protect the inner cells of leaves against bright sunlight, particularly the sun's ultra-violet rays. Another view of their possible function is that they convert some of the sun's rays into heat energy which protects the cells in which these pigments are present

from injury by low temperature. Both of these views are theories, however, with little experimental evidence in support of them.

The most striking phase of leaf colors is found in the autumnal transformation of summer greens into brilliant yellows, oranges, and scarlets. A number of factors is involved in the physiological processes responsible for these changes. These will be described in some detail in the following paragraphs.

When abscission and corky layers form at the bases of petioles, they interfere with the conduction of materials into and away from leaf blades. The chlorophyll in the leaf blades is decomposed by light, as described above, but is not simultaneously synthesized, for the raw materials — nitrogen, magnesium, and other substances — necessary for its manufacture move much more slowly into the leaf blades. As a result of its destruction and the failure of its re-formation, chlorophyll disappears from leaf blades. As the chlorophyll vanishes, the yellow and orange colors of xanthophyll and carotin become visible, for they are no longer masked by chlorophyll and they are not decomposed by light as is chlorophyll.

The flaming red colors characteristic of the autumn leaves of sumacs, hard maples, oaks, and numerous other species of plants are attributable to the formation of anthocyanins not previously present in the leaves, probably as a result of the accumulation of certain waste products. The details of the development of these pigments are not known, but their appearance is correlated with the presence of considerable quantities of sugars in leaves. Light seems to promote the formation of these red pigments, as do also very sudden drops in temperature. If the main vein of a leaf is severed in early autumn, the portion of the blade beyond the cut becomes a deeper red than other portions of the leaf, for the disjunction of the vein prevents sugars from leaving this part of the leaf and thus promotes anthocyanin formation. The sudden decrease in temperature usually accompanying frost inhibits the removal of sugars and often deepens the colors of the anthocyanins in leaves, but the frequent appearance of yellow, orange, and red colors *before* the first frost indicates that frost is not essential to the development of these hues.

With the death of all the cells of leaves, these various pigments disintegrate, and leaves become brown in color before they fall. When killing frosts come very early and very suddenly in autumn, the tissues of leaves are quickly killed and immediately become brown without passing through a series of yellow, orange, and red hues.

3. PHOTOSYNTHESIS

Photosynthesis is the fundamental process of food manufacture in nature and is the primary physiological process performed by leaves. The important product of photosynthesis is **sugar,** which, in addition to the direct uses which it serves, is the basic food from which all other kinds of foods in nature are manufactured. Thus, photosynthesis makes possible the existence of all plants (except a few species of bacteria) and all animals. If any one physiological process of plants can be designated as "most important," photosynthesis is that process. Such a statement must be made guardedly, however, for without the processes of osmosis, translocation, chlorophyll-formation, etc., photosynthesis could not occur. Evaluated in terms of the importance of its products, photosynthesis may seem more important than these other processes but since all of the physiological changes of living organisms are interrelated, no one can be regarded alone without reference to associated processes.

Photosynthesis proceeds only in the chloroplasts of green plant cells and only in the presence of light. The raw materials which are combined in the process are **carbon dioxide** and **water,** and the products are usually **sugar** (glucose, or grape sugar) and **oxygen**. These substances combine and are formed in fixed proportions represented by the equation.

$$\text{Light energy} \; + \; 6CO_2 \; + \; 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$
$$\text{(carbon dioxide) (water) \quad (glucose) \quad (oxygen)}$$
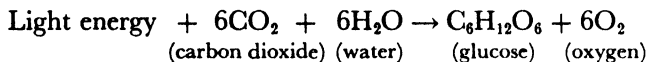
This formula states that six molecules of carbon dioxide combine with six molecules of water to form one molecule of glucose and six of oxygen. This formula merely indicates the reacting proportions and does not show anything of the doubtless very complex chemical reactions involved in the transformation of the raw materials into the products. Little is known of these intermediate chemical processes and thus the formula presented above must be interpreted as indicating merely the beginning and concluding phases of photosynthesis.

The actual weights of the raw materials used and the products manufactured in photosynthesis are:

$$264 \text{ g. } CO_2 + 108 \text{ g. } H_2O \rightarrow 180 \text{ g. } C_6H_{12}O_6 + 192 \text{ g. } O_2.$$
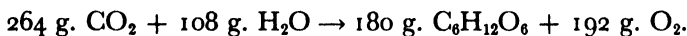
In most plants, the first visible product of photosynthesis is starch, which is quickly formed from glucose as this sugar is manufactured in photosynthesis. In some plants, particularly such monocotyledonous plants as lilies and bananas, oils rather than starches are the first visible

products of photosynthesis. Some plant physiologists believe that cane-sugar (sucrose) is the first product of photosynthetic activity, but the evidence seems to indicate that in most plants glucose is the first sugar formed in photosynthesis and that it may be transformed with the leaf cells to sucrose, starch, oils, or other more complex substances.

The carbon dioxide used in photosynthesis is obtained by leaves from the external atmosphere, of which it makes up approximately .03% to .04%, or 3 to 4 parts per 10,000 parts of air. Carbon dioxide is added to the air as a result of the combustion of fuels, of volcanic action, of rock weathering, of the decay of organic substances, and of plant and animal respiration. Simultaneously some of the carbon dioxide in the air is used in photosynthesis, so that the proportion of this gas in the air fluctuates but little. Carbon dioxide enters leaves through the stomata of leaves by simple gaseous diffusion from the region of higher CO_2 concentration (the external air) to that of lower CO_2 concentration (the air inside the leaf spaces).

Each stoma is enclosed by a pair of guard cells, turgor changes in which produce expansion or contraction of the cells and thus open or close the stoma. The inner-guard cell walls, those bordering upon the stoma, are much thicker than the outer walls, those which touch upon other epidermal cells. When the turgor pressure within guard cells increases, the outer, thinner walls expand more rapidly than the thick inner walls and pull the inner walls away from each other, thus opening the stoma. With a decrease in the turgor pressure, the thick inner walls straighten and move toward each other, closing the stoma. The factors responsible for turgor changes in guard cells are not fully known; it has been demonstrated, however, that light promotes the conversion of starch within guard cells to sugars. The increase in the concentration of sugars decreases the relative concentration of water within the guard cells which absorb water from surrounding cells and thus expand and open the stomata. The stomata of most plants are usually open to the greatest extent during the day; during this time, photosynthesis proceeds actively. At night, the concentration of sugars with guard cells decreases and water leaves the cells, which contract and close the stomata.

The CO_2 which diffuses into a leaf is used up in photosynthesis when it enters the leaf cells and thus its concentration is continuously lower inside the air spaces of the leaf than it is outside, as long as photo-synthesis proceeds. When the molecules of carbon dioxide reach the walls of the mesophyll cells they go into solution in the water which saturates these walls and then diffuse in solution into the protoplasm

of these cells, reaching the chloroplasts where photosynthesis takes place. Green plants ordinarily have abundant light, chlorophyll, and water for photosynthesis, but the supplies of CO_2 available to them are limited by the small concentration of this gas in the atmosphere. Because of the fact that the speed of the photosynthetic process under conditions of abundant light and moisture is usually limited by the low concentrations of carbon dioxide available, carbon dioxide is often termed the "limiting factor" in photosynthesis. It has been shown experimentally that an increase of as much as 20 times in the normal atmosphere concentration of carbon dioxide induces a corresponding increase in the rate of photosynthesis in some plants. Several greenhouses in this country are equipped with devices to increase the carbon-dioxide content of their air, for a more rapid rate of photosynthesis results in more rapid growth and frequently in greater yields of flowers, fruits, vegetables, etc. Experiments have also shown that the yield of certain field crops is increased if the air about them is enriched by the addition of carbon dioxide from pipes laid in or on the ground. Such "aerial fertilization" is still largely experimental, but may in the near future become of widespread practical importance in crop culture.

The water used in photosynthesis is absorbed by the roots of plants and moves upward into leaf blades through the xylem elements of roots, stems, petioles and leaf stems, as described in earlier chapters.

Photosynthesis is an energy-storing process and thus must have available for its operation externally supplied energy. This energy which makes photosynthesis possible is light energy which comes from the sun, or under artificial conditions, from electric lights. Of the various types of radiations, which reach green plants from the sun, the visible rays are most important in promoting photosynthesis, especially the red rays and to a lesser extent the blue-violet rays of the spectrum. Green and yellow rays are of relatively little value in furnishing energy for photosynthesis, for they are mostly reflected and transmitted by leaves, not absorbed as are the red and blue rays. Only those rays which are absorbed by the green cells of leaves can furnish energy for photosynthesis. Of the total solar energy reaching the leaves of plants, from .5% to 3%, depending upon other environmental factors and upon the species of plant in question, is actually transformed into the stored energy of sugar in photosynthesis. The remainder of this energy is reflected from the leaf surfaces, passes through the leaves, or is absorbed as heat. This process is thus exceedingly inefficient. If, however, one contemplates the enormous numbers of leaves on the earth's surface

and remembers that green plants adequately nourish themselves and in addition all of the earth's animals, the inefficiency of this light utilization becomes insignificant. One of the most fundamental facts of nature is this: *that green plants alone are able to convert the energy of sunlight into forms which can be utilized by plants themselves and by animals.* Photosynthesis may thus be interpreted as a method of making a portion of the sun's energy available for nutritional use by organisms, and sugars and the other foods derived from them may be regarded chiefly as stored energy which living organisms can utilize.

In the manufacture of 180 grams of sugar in photosynthesis, 674 calories [1] of active light energy are converted into the potential, chemical energy of food. A single gram of sugar contains approximately 3.75 calories of potential energy, which can be released in the process of respiration, as will be described in the next chapter. One investigation has estimated that a single acre of corn plants in Illinois makes an average of about 200 pounds of sugar per day during a single growing season and that in the total amount of sugar formed during the growing season about 33,000,000 calories of energy are stored.

The manner in which chlorophyll is involved in photosynthesis is not entirely understood. Chlorophyll acts as a light screen which absorbs the red, blue, and violet rays of sunlight and thus acts as an energy-absorber for sugar manufacture. It is probable also that chlorophyll is involved chemically in the process of photosynthesis for it is known to form an unstable union with carbon dioxide. The details of this probable chemical involvement of chlorophyll in photosynthesis are not known.

A portion of the oxygen formed in photosynthesis diffuses outward through the open stomata in accordance with the simple laws of diffusion. The liberation into the air of oxygen formed in photosynthesis constitutes the principal method of counterbalancing the oxygen used by plants and animals in their respiration and of maintaining thus a fairly constant proportion of this gas in the atmosphere. Another portion of this oxygen is used within leaves and probably other parts of plants in oxidation processes involved in respiration, as will be described in the next chapter.

The speed at which glucose is manufactured in photosynthesis varies in different species of plants and with changing environmental conditions. In bright light and warm temperature, leaves of most plants

[1] A calorie ("large calorie") is the amount of heat required to raise 1000 grams (about 1 quart) of water one degree centigrade.

manufacture sugars at the rate of .5 to 1.8 grams (a gram is about $\frac{1}{28}$ of an ounce) per hour per square meter (slightly more than a square yard) of leaf surface. These values represent averages and may fluctuate from hour to hour during the day. The glucose manufactured in photosynthesis may be utilized in a variety of ways. Some of it is oxidized in leaf cells or cells in other parts of plants in furnishing energy (respiration), some of it is used in the synthesis of other kinds of foods, some glucose is converted into starch, the most common storage carbohydrate food in plants, and some of it is used to form cellulose and other compounds necessary for growth and for the formation of new protoplasm (**assimilation**).

In most species of plants, as glucose molecules are formed in photosynthesis, they are converted almost immediately into starch which accumulates in leaf cells during the light part of the day. This behavior is advantageous, for starch is insoluble in water and thus does not affect the osmotic properties of cells, as sugar does. Furthermore, the conversion of sugar into starch results in a decrease in volume; that is, the starch does not occupy as much space as do sugars. During the night, when photosynthesis does not take place, much of the starch stored in the mesophyll cells during the day is transformed back into sugars, a portion of which is translocated through the veins and petioles to the stems and other portions of plant bodies to be utilized in the various processes described in the preceding paragraph.

The rate at which photosynthesis proceeds depends upon a number of factors, chief among which are: *temperature*, which is most favorable between 65° and 85° F., *carbon dioxide* as explained above, *light* intensity and quality, *water* supply available, *chlorophyll* concentration within the mesophyll cells, and *oxygen* concentration. Sunlight is most effective of all kinds of light in promoting photosynthesis and full sunlight is more effective than any of its component rays. Photosynthesis is carried on by the energy of artificial light but not so rapidly as under sunlight, largely because of the lower energy values of most kinds of artificial light. Although oxygen is not a raw material in photosynthesis, it is necessary for the normal functioning of the protoplasm of green plants and is thus a factor indirectly influencing photosynthesis.

The leaves of most plants may be considered as rather efficient photosynthetic mechanisms. They are usually broad and thin, and thus light penetrates readily all cells of the mesophyll. Their epidermal layers contain numerous stomata, through which carbon dioxide diffuses into the intercellular spaces of the mesophyll. These spaces afford ready paths

of diffusion of carbon dioxide to all green cells of leaves. Further, the numerous ramifications of the vein systems carry water to all cells of leaves. Finally, the numerous chloroplasts of the mesophyll cells constitute the actual machinery in which the transformation of water and carbon dioxide into sugar is achieved.

4. TRANSPIRATION

Transpiration is the evaporation of water from the aerial parts of plants, especially the leaves. This process goes on at all times, except possibly when the air is saturated with moisture during or immediately following rains. The quantities of water lost by transpiration are often incredibly great. It has been determined that a single sunflower plant during a growing season of approximately 140 days loses about 145 pounds of water by evaporation from its aerial portions, an average daily loss of more than 1 pint of water. A single corn plant has been found to lose by transpiration over 50 gallons of water (more than 400 lbs.) during its life span of 100 days. An acre of corn plants, transpiring in this same degree, evaporates into the air over 300,000 gallons of water in a 100-day growing season. Calculations of the quantities of water transpired by large apple trees indicate that a single, full-grown apple tree loses by evaporation as much as 1800 gallons of water in a growing season of about six months. A study of these figures indicates how vast expanses of vegetation, such as large forests, are able to exert marked influences on the climate of the regions in which they grow. The tremendous amounts of water vapor transpired by such extensive masses of vegetation affect air temperatures, increase the moisture content of the air, and thus influence the frequency and quantity of rainfall.

Students should remember that these figures represent water losses by evaporation in only a few species of plants and that the amounts of water transpired by plants vary in different species, and from minute to minute as environmental conditions fluctuate.

The quantities of water which are lost by transpiration are very great as compared with the amounts of water used by plants in the synthesis of foods and other organic compounds. Botanists have devised an expression of this relationship by dividing the total quantity of water absorbed by the total final dry weight of the plant in question. This quotient, called the **water requirement,** represents the number of pounds of water required by a plant to manufacture one pound of

dry or solid substance. The water requirements of a number of plants
are stated below:

Sorghum	250	Potato	636
Corn	350	Cucumber	713
Red Clover	460	Alfalfa	900
Wheat	500		

Alfalfa is noteworthy in that it has probably the highest water require-
ment of all of the commonly cultivated crop plants. The water require-
ment varies in different species of plants, as the table indicates, and
also varies to a slight extent under changing environmental conditions,
though not very greatly. The water requirement is thus to be regarded
as a rather characteristic hereditary trait for each species of plant,
expressing a complex of structural and physiological relationships be-
tween water absorbed and water used in the synthesis of dry matter.
Most of the water absorbed obviously is not used in food manufacture,
but is lost by transpiration from the aerial parts of plants.

Ordinarily about 90% or more of the water which evaporates from
leaves passes out into the air through stomata; the remainder of the
water vapor lost diffuses outward through the cuticles of the epidermal
layers. The former type of transpiration is termed **stomatal**, the latter
cuticular transpiration. The relative amounts of water vapor lost by
these two methods show that stomatal transpiration is by far the more
abundant and hence the more important of the two.

The actual conversion of liquid water into water vapor does not
occur at or through the stomata, for the latter are merely holes in the
epidermal layers of leaves. Liquid water passes into vapor from the wet
walls of the mesophyll cells of leaves at the places where such walls are
exposed to the intercellular spaces of the mesophyll tissues. As water
vapor collects in these spaces, it moves outward through the stomata
into the external air, in accordance with the laws of simple diffusion.

Transpiration proceeds more rapidly during the day than at night,
chiefly because the stomata are open widest during the day and also
because the environmental factors which prevail during the day favor
rapid evaporation of water. At night, when stomata are partially or
wholly closed, the rate of transpiration is considerably less than that
during the day. The nocturnal rate of evaporation from leaves is
frequently as low as 1 to 3% of the diurnal rate.

The principal external factors which influence the rate of tran-
spiration in plants are *light, temperature, wind velocity, humidity,* and soil
factors.

Transpiration is more rapid in bright light than in diffuse light or in darkness, partly because certain light rays raise the temperature of leaf cells and thus increase the rate at which liquid water is transformed into vapor, partly because bright light is the chief stimulus which causes stomata to open. The exact nature of the action of light on the guard cells of leaves is not known, but, as has been described above, light brings about an increase in the sugar content of these cells, resulting in a higher osmotic concentration in them and a consequent passage of water into the guard cells from other leaf cells with lower osmotic (relatively higher water) content. With the increase in turgor, the guard cells expand and open the stomata between them. At night when the sun sets, the sugar content of guard cells decreases, water moves out from them, and they decrease in volume, closing the stomata partially or wholly as they shrink. Variations in the intensity of light from hour to hour cause continual changes in the sizes of the stomata of leaves and thus influence the rate of transpiration. Because of its twofold effect upon water evaporation from leaves, light may be considered the most important of the external factors influencing transpiration.

High temperatures favor more rapid transpiration, not only because evaporation occurs quickly in warmer air but also because warm air is capable of holding more water vapor than is cold air. At moderate or low temperatures, the rate of transpiration is markedly less than it is when the temperature of the surrounding air is high.

When the external atmosphere is very humid, the evaporation of water from leaves is reduced, for the difference in water vapor concentration in the inner spaces of leaves and in the outside air is so slight that the outward diffusion of water molecules from leaves is very slow. The rate of transpiration is roughly proportional to atmospheric humidity; thus, the drier the air, the more rapid is the rate of water evaporation from leaves. It is a known fact that plant organs, particularly leaves, become larger when they grow in humid atmosphere than in dry air. The greater the atmospheric humidity, the lower the rate of transpiration and the greater is the amount of water retained within the plant for growth.

When there are no breezes, the motionless air near transpiring leaves becomes very humid and, as a result, the rate of water evaporation decreases. Moving air currents continually bring fresh, dry masses of air in contact with leaf surfaces and thus maintain a high rate of transpiration. However, the rate of transpiration is not directly proportional

to wind velocity, for closure of the stomata frequently begins when the wind velocity exceeds 25 or 30 miles per hour, and thus the transpiration rate may be lowered at high velocities.

Soil temperature, the solute concentration of the soil solution, the water content of the soil, and other soil factors influence the rate of transpiration indirectly in that they affect the rate at which roots absorb water. If plants cannot absorb water readily, the rate of their transpiration is correspondingly low. If water is more easily absorbed, the transpiration rate is higher.

Other factors of importance in controlling the rate of transpiration are those inherent in the physiological and structural organization of plants. Among these internal factors regulating transpiration is stomatal behavior. It might seem at first consideration that plants can control in large degree the rate of water evaporation from their leaves by closing their stomata, for these apertures are easily regulated by their surrounding guard cells. However, the stomata of plants are singularly ineffective in reducing water-vapor loss, for so long as leaves are turgid and are exposed to light, their stomata remain open. Only when leaves begin to wilt and the guard cells lose their turgidity are the stomata closed. The inner walls of guard cells, that is, those which border upon the enclosed stoma, are thicker than the outer walls, which border upon other epidermal cells. When the turgor pressure within guard cells increases, the outer, thinner walls expand more rapidly than the thicker inner walls and the inner walls are pulled apart, opening the stoma. When the turgor pressure within these cells decreases, the inner walls tend to come together and close the stoma. One investigator has estimated that nearly all of the reduction in transpiration caused by stomatal closing occurs when the stomata have closed to about 2 or 3% of their full apertures. Thus stomatal regulation of transpiration occurs only after evaporation has proceeded to such an extent that wilting begins; such control may be regarded as only partially effective.

The colloidal materials in protoplasm hold water very tenaciously and when transpiration has proceeded for some time at a rapid rate, the water-retaining power of these colloids frequently causes a marked decrease in transpiration rate. Many desert plants, such as various species of cacti and acacias, have mucilaginous, gummy materials in large quantities in their tissues. These substances are colloidal in nature and are especially effective in retaining water against various drying forces. One experimenter found that tubers of a desert gourd were able to·retain a part of their water for almost seven years after they were uprooted and placed on a laboratory shelf to dry.

Structural modifications in many species of plants growing in desert soils of low water content frequently conserve water. Plants which grow in such regions and which possess structural devices which reduce transpiration are termed **xerophytes** to distinguish them from **hydrophytes** (plants growing in water) and **mesophytes** (land plants growing in regions with moderate to abundant rainfall). Among the characteristic structural features which conserve water in xerophytes are: heavy layers of cutin on leaves and stems, reduced number of stomata, stomata sunken in pits below the surfaces of leaves, abundance of water-storage tissues, and reduction in size or absence of leaves. Some xerophytes produce leaves during the rainy season and drop them as soon as the rains cease and dry weather begins. In many grasses, such as corn, the leaves roll inward laterally and thus reduce the amount of leaf surface during dry periods. There are numerous other structural and physiological features which reduce or control transpiration in plants; it should be emphasized, however, that xeromorphic structure does not always result in reduced transpiration, for some xerophytes lose water very rapidly.

The question of the importance of transpiration to plants is an important and much debated one. It has been suggested that transpiration is significant in lowering the internal temperatures of leaves on warm days, since evaporation of liquids is known to exert a cooling effect. Numerous measurements of the temperatures of leaf tissue show conflicting results and justify only one general conclusion: namely, that in some species of plants, transpiration lowers the temperature of leaves on hot days several degrees below that of the surrounding air, and that in the leaves of other species of plants a cooling effect of transpiration is not demonstrable. When leaf temperatures are lowered by transpiration, the internal temperatures are rarely more than 3 or 4 degrees lower than those of the outside air. Thus, it seems safe to state that the possible cooling effect of transpiration is not apparent in all plants and that when it is measurable, it is so slight as to be of doubtful importance.

It has been argued by some plant physiologists that transpiration may be regarded as having a positive beneficial effect in plants in that it furnishes the pull in leaves which is principally responsible for the rise of sap. It should be emphasized, however, that if there was not such tremendous water loss from leaves, plants would not need to lift such large quantities of water into their leaves. It has not been demonstrated experimentally, whether or not the rise of sap is inextricably connected

with transpiration. There is a tendency on the part of many plant physiologists to belittle the importance of transpiration in sap rise and to consider the process as one chiefly or entirely detrimental.

It is sometimes stated that rapid transpiration favors a correspondingly rapid absorption of mineral salts from soil. There is little experimental evidence in favor of such a supposition, although it is true that rapid transpiration promotes the upward movement of salts in the xylem *after* they have entered the roots of plants.

The chief disadvantage to plants of transpiration lies in the fact that it frequently causes excessive loss of water, resulting in wilting and often death. If the rate of water absorption by roots equals or exceeds that of transpiration, no wilting occurs, but if transpiration overbalances water absorption for very long, wilting is inevitable.

Transpiration is sometimes called "unavoidable," a statement which is doubtless true, for plants have no way of preventing the escape of water vapor from the leaves when their stomata are open. It should be emphasized here that the primary importance of stomata is their admission to mesophyll cells of the carbon dioxide necessary for photosynthesis, not the regulation of water loss. Stomata are open and admit carbon dioxide in light during the day. Simultaneous with the intake of carbon dioxide is the unavoidable escape of water molecules from the intercellular spaces of leaves.

5. TRANSPIRATION AND PLANT CULTIVATION

Farmers, horticulturists, and others engaged in large-scale plant culture employ certain practices which are intended to reduce transpiration. One of the commonest of these is the removal of weeds from the vicinity of the cultivated plants. Weeds, like other plants, transpire and thus deplete the water supplies of the soil. When weeds are removed, the water in the soil which they would have used is reserved for the use of the desired plants. Weeds are removed for other reasons as well; they shade the cultivated plants and thus interfere with their photosynthetic activities, they use soil minerals which are thus lost to the crop plants, and they crowd and frequently stunt the root growth of cultivated plants.

Horticulturists whitewash their greenhouses during the summer to reduce the intensity of sunlight and to lower the greenhouse temperature. They usually water the walks, floors, and walls of the greenhouses several times during the summer days to maintain a high degree of

Fig. 118. Windbreak plantation in Champaign County, Illinois. The windbreak planting was made in co-operation with the extension service of the College of Agriculture, University of Illinois.

humidity in the air. These practices result in a general decrease in the rates of transpiration of plants growing in these houses.

When horticulturists propagate plants from cuttings, they remove some of the leaves of the cuttings when the latter are placed in the cutting benches or they cover them with glass jars. The reduction of leaf surface in the first case diminishes water loss from cuttings and thus prevents their wilting. The glass jars prevent air currents and maintain very humid air around the cuttings, thus decreasing transpiration and at the same time allow light to reach the leaves which can thus manufacture sugars.

One of the major reasons for windbreaks of trees (Figure 118) planted about fields and gardens, particularly in regions of dry summers, is to break the force of hot, dry winds and thus to prevent excessive transpiration from the leaves of the garden or orchard plants growing behind the windbreaks. In addition, windbreak trees offer a certain amount of mechanical protection against the forces of strong winds. State and federal agencies concerned with problems of reforestation, soil conservation, and agricultural improvement have planted shelter belts of sturdy, drought-resistant trees in many parts of the country to bind the soil and to protect crops.
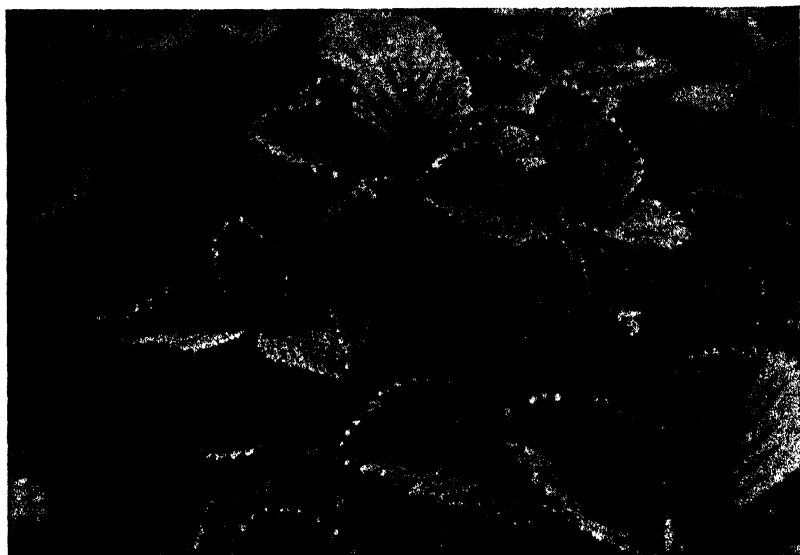
Fig. 119. Guttation in strawberry leaves.

6. GUTTATION

Guttation is the exudation by aerial parts of plants, chiefly leaves, of water in liquid form. Guttation occurs usually when environmental conditions are such as to check transpiration, particularly during cool nights following hot days when the air is very humid. Drops of water appear along the margins of leaves, usually as a result of exudation through special structures known as **hydathodes**. Guttation occurs frequently in the leaves of strawberries (Figure 119) and roses at night or in the early morning hours following cool, humid nights, especially when the available soil moisture is abundant. In many plants, guttation is never apparent and in others it occurs only rarely. The exudation of water droplets is a direct result of the existence of root pressure within a plant; high atmospheric humidity and abundant available soil moisture favor the development of root pressure and the process of guttation. Guttation should probably be considered a resultant of other physiological processes, not as a process of positive physiological significance in plants. The quantities of water lost by plants through guttation are relatively insignificant as compared with the amounts of water lost through transpiration.

SUMMARY

1. Deciduous trees and shrubs drop their leaves at the end of their growing season and thus pass a portion of each year without leaves. Evergreens shed small numbers of their leaves at intervals and thus always have some leaves on their stems.

2. Leaves fall as a result of the development of an abscission layer across the base of the petiole and the subsequent disintegration of this layer.

3. The predominant color of leaves is green and is due to the presence of chlorophyll. In the autumn, chlorophyll disappears from leaves and the yellowish pigments, xanthophyll and carotin, masked earlier by the chlorophyll, become apparent. The formation of red and purple pigments in leaves in autumn follows the development of certain disintegration products and is in some manner related to the sugar content of leaves.

4. Photosynthesis is the manufacture of grape sugar from carbon dioxide and water in the presence of light through the mechanism of chlorophyll. The raw materials and end products are represented in the formula:

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$
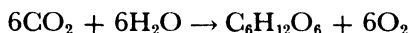
5. The sugar thus manufactured may be converted into starch or oil or other types of compounds or used directly as a source of energy.

6. Green plants are able to convert the active energy of sunlight into the stored or potential energy of foods.

7. The rate at which photosynthesis occurs is influenced by a great number of factors.

8. Leaves may be considered rather efficient photosynthetic mechanisms.

9. Transpiration is the loss of water vapor from the aerial parts of plants.

10. Transpiration constitutes an ever-present danger, for an excess of transpiration over water-absorption by roots leads to wilting and often death.

11. Transpiration exerts a cooling effect upon the internal tissues of some leaves, but such cooling effect is probably of little significance.

12. Transpiration varies with changes in light intensity, wind velocity, atmospheric humidity, etc.

13. Certain internal factors, such as leaf anatomy, imbibitional forces of protoplasmic colloids, etc., influence the rate of transpiration.

14. Hydrophytes are plants which grow partly or wholly submerged in water; xerophytes grow in soils of low moisture content; mesophytes grow in soils of moderate available water content.

15. Transpiration apparently provides the principal force which is responsible for the rise of sap. However, if there were not such tremendous water losses from leaves by transpiration, plants would not need to lift such large quantities of water into their leaves.

16. The chief importance of stomata and guard cells lies in their admitting carbon dioxide to the interior of leaves. They are not very effective in regulating transpiration until leaves have already begun to wilt.

17. Various methods are used by horticulturists, orchardists, etc., to prevent excessive transpiration from the leaves of cultivated plants.

18. Guttation is the exudation by aerial parts of plants of water in liquid form.

Metabolism

THE TERM **metabolism** includes all of the chemical changes which are involved in the physiological activities of living organisms. Certain phases of metabolism involve the synthesis of foods and other organic substances used for energy and for the construction of tissues; these processes are known collectively as **anabolism,** or constructive metabolism. Chemical reactions which result in the breaking-down of certain of these elaborated substances with the release of their stored energy are called collectively **catabolism,** or destructive metabolism. Anabolism is involved in all increases in the amount of protoplasm in an organism, as in processes of growth and reproduction, and also in the replacement of "worn out" parts of protoplasm. Protoplasm is in a continual state of change; certain compounds in it are being broken down as others are being synthesized. Thus, the maintenance of protoplasm, aside from processes of growth, involves unceasing metabolic activity. All the anabolic processes in living organisms require energy, just as the construction and operation of elaborate physical machines — e.g., aeroplanes — require energy. The ultimate source of the energy which makes possible the constructive phases of metabolism is the sun, whose active or kinetic energy is transformed in photosynthesis into the stored or potential energy of foods. The energy stored in foods is released in respiration, the principal catabolic activity of living organisms. The energy thus set free is used in many ways — repair, growth, movement, reproductive activity, etc. Because anabolic processes require energy, they are sometimes described as *endothermic* ("heat going in"), whereas catabolic activities, which usually release energy from organic substances, are termed *exothermic* ("heat going out").

I. ANABOLISM

A. FOODS

The fundamental anabolic phase of green plants is photosynthesis, discussed in detail in the preceding chapter. A part of the sugar manu-

factured in photosynthesis is used immediately to supply energy for various other physiological processes of cells; other portions of this sugar are utilized in the construction of other kinds of foods and other organic substances such as chlorophyll, xanthophyll, carotin, suberin, etc. All of the processes involved in the synthesis of these materials are anabolic in nature.

The word "food" is frequently used to designate all types of substances which enter the bodies of living organisms and which are used by them. In this sense, "food" is commonly used by florists, horticulturists, and farmers to refer to the mineral salts and other inorganic materials absorbed by plants from the soil. Most physiologists prefer a more restricted use of the word "food" — *to refer, namely, to those organic materials used by living organisms as sources of energy or of building materials for the construction of new tissues.* In terms of this more limited definition, mineral salts and other relatively simple inorganic substances absorbed from the soil are not foods, but are the *raw materials* from which green plants make foods.

The mineral salts absorbed from the soil by plants and used in the manufacture of foods and other organic substances in plants are chiefly the nitrates, phosphates, and sulfates (and certain other salts in smaller quantities) of calcium, magnesium, potassium, and of several other minerals, chiefly iron, copper, aluminum and possibly others, in much smaller quantities. These mineral substances are transported chiefly through the xylem and possibly through the phloem into leaves and other portions of plants in which the syntheses of organic substances occur. Carbon, which forms an integral part of all organic compounds, enters plants chiefly in the form of carbon dioxide from the air, as described in the preceding chapter. Oxygen, likewise present in virtually all organic compounds made by plants, enters plants partly as a constituent of carbon dioxide and of water, partly as free oxygen from the external atmosphere. Oxygen enters the roots of plants from the air held in the soil and diffuses into leaves from the air surrounding them. Hydrogen, also a constituent of the organic substances manufactured by plants, is supplied by water through the process of photosynthesis.

The minerals and other solutes which are absorbed from the soil and used by plants enter into a variety of chemical reactions and combinations. Phosphorus and sulfur, for example, are important constituents of many kinds of proteins; nitrogen is an essential element in the molecules of proteins, chlorophyll, and many other substances manufactured

by green plants; magnesium is a necessary constituent of chlorophyll; iron, though it is not present in the chlorophyll molecule, is required for chlorophyll synthesis; calcium is present in the cell walls of most species of plants and in addition seems to influence the building-up of protoplasm, etc. The study of the specific physiological effects of the various minerals absorbed by plants from the soil constitutes a large and important field of plant physiology. The results of numerous investigations upon the nutrition of green plants show that approximately 15 elements are essential to normal growth and development — carbon, oxygen, hydrogen, nitrogen, phosphorus, potassium, sulfur, magnesium, iron, calcium, boron, manganese, copper, aluminum, zinc, and possibly several others as well.

Different species of plants require these mineral salts in different proportions and remove them from soils in varying quantities. If one crop is grown repeatedly on the same soil, the minerals absorbed in greater abundance by this crop are seriously depleted. The practice of crop-rotation — that is, the growing of different crops in successive years on the same land — reduces this danger, for different kinds of crop plants absorb soil minerals in varying quantity and thus are less likely to deplete the supply of any one mineral or groups of minerals. If soils are to be continuously productive, however, compensation must be made to them for the minerals which crops absorb, for every harvest depletes the raw materials of the soil. This restoration of sulfates, nitrates, phosphates, and other salts can be achieved by two methods: the addition to soils of commercially prepared fertilizers, containing these salts which are usually derived from animal wastes (manures), bone meal, dried blood, etc., and the plowing under of stubble, dead leaves, and certain crops, such as alfalfa, soybeans, etc., which contain large amounts of nitrogenous materials. In the latter treatment, the decomposition of the organic substances present in the plant tissues results in the accumulation in the soil of the mineral salts, the presence of which is necessary for the continued fertility of the soil. The burning of dead leaves in the autumn and of straw, stubble, etc., is wasteful, for many substances in them which would restore nitrogenous compounds to the soil are dissipated into the air in gaseous form.

Recently there has been a revival of interest in scientific and popular circles in the culture of plants in water solutions of minerals. Many greenhouse crops — tomatoes and roses, for example — are grown successfully with large yields in water with dissolved minerals, in place of soil. In many cases the yields are larger than those resulting from the

growth of the same plants in soil. There are certain advantages in this method of plant growing — namely, better regulation of the mineral requirements of plants, more uniform fruits or flowers, elimination of deleterious effects of toxic materials sometimes present in soils, better control of plant diseases, growth of crops out of their normal outdoor seasons, etc. There are likewise certain disadvantages, one of which is the necessity of providing for the frequent aeration of roots, another of which is the great expense involved in the construction of tanks, the purchase of pure chemicals, the installation of pumps and other required machinery, etc. The commercial growth of plants in such chemical solutions is at present limited by the expenses mentioned above chiefly to the production of fruits and flowers of extra-fancy quality, especially in off-seasons, when such crops are likely to command very high prices. Soils probably will always form the chief substrates for the cultivation of crops for most of mankind. Despite colorful accounts of "chemical gardening" and of "hydroponics" as "new sciences" in the pages of popular magazines, water cultures have been known and used by plant physiologists for more than seventy-five years for the scientific study of plant nutrition. Most of the information concerning the functions in plants of the various chemical elements absorbed from the soil has been derived from the growth of plants in water cultures of different chemical composition. By studying the growth and physiological activities of plants growing in solutions containing a wide range of chemical elements and comparing them with the growth and activities of plants growing in solutions lacking various of these elements, plant physiologists have been able to determine the specific roles which these elements play in the lives of plants. Such studies have led to many practical applications, particularly in the correction of chemical deficiencies in various types of unproductive soils and in the increase in productivity of such soils.

As described previously, carbon dioxide and water are transformed into sugar in photosynthesis, and this sugar is then utilized in the elaboration of other kinds of organic compounds in plants. In the manufacture of many of these other organic substances, mineral elements are important either as constituents of these substances or as chemical regulators of their synthesis.

There are three kinds of foods manufactured by living organisms from raw materials of the kinds described above: **carbohydrates, fats, and proteins.**

Carbohydrates are always composed of carbon, hydrogen, and

oxygen, with the hydrogen and oxygen in the same proportion (2 to 1) as they are in water. Most carbohydrates in plants contain in their molecules six carbon atoms or some multiple of six; common carbohydrates in plants are glucose, or grape sugar ($C_6H_{12}O_6$), fructose, or fruit sugar ($C_6H_{12}O_6$), sucrose, or cane sugar ($C_{12}H_{22}O_{11}$), maltose, or malt sugar ($C_{12}H_{22}O_{11}$), and starch and cellulose, both with the basic formula ($C_6H_{10}O_5$)$_n$. The fact that different carbohydrates (e.g., glucose and fructose) often have the same chemical formula means that the differences between them are attributable to differences in the *arrangement* of their constituent atoms, *not* to differences in the kinds or number of their atoms present. Many carbohydrates, such as sugars, are soluble in water and can thus move readily from one part of a plant to other parts. Starch and cellulose, however, are insoluble in water and thus cannot be translocated in plants, unless they are converted into sugars. Starches are the commonest reserve carbohydrates in plants and are found stored in the form of tiny grains in many kinds of cells in fruits, such as bananas, in the cells of seeds, such as corn and wheat, of various types of roots (carrots) and of stems (potato tubers). Sugars are also stored in considerable quantities in the tissues of certain plants, as in sugar cane, sugar beet, and sugar maple. The chief uses of carbohydrates in plants are: to supply energy (sugars), to furnish the fundamental materials from which other organic substances, especially fats and proteins, are made, and to build the structural framework of plants (cellulose).

Fats and oils are similar to carbohydrates in that they are composed of the same chemical elements: carbon, hydrogen, and oxygen. The arrangement of the atoms of these substances in fat molecules differs markedly from that in carbohydrate molecules, and the proportion of hydrogen to oxygen in fats is much higher than the 2-to-1 ratio of carbohydrates. The chemical formulas of two plant fats, stearin and palmitin, are respectively $C_3H_5(CO_2C_{17}H_{35})_3$ and $C_3H_5(CO_2C_{15}H_{31})_3$. These formulas show the relatively small proportion of oxygen in these substances. It is largely because of this low percentage of oxygen that fats are able to provide about twice as much energy as sugars, weight for weight, for fats can be oxidized (burned) to a greater extent, since they contain little oxygen, than can sugars, which have higher oxygen contents. In plants, fatty substances occur most frequently as oils — that is, they are liquid at ordinary temperatures. All fats and oils are insoluble in water and leave translucent grease spots on paper. Fats are chiefly reserve foods which are stored in various plant structures,

especially seeds (peanut, coconut, castor bean) and fruits (banana, avocado, paw-paw). When these reserve foods are about to be utilized, they are usually converted into sugars. Certain complex fatty compounds are actual constituents of living protoplasm, particularly in cytoplasmic membranes.

Proteins are probably the most complex organic substances in living organisms. Their molecules are exceedingly large, as is shown by two plant proteins, zein from corn and gliadin from wheat, the formulas of which are respectively $C_{736}H_{1161}N_{184}O_{208}S_3$ and $C_{685}H_{1068}N_{196}O_{211}S_5$. Proteins, like fats, are made from carbohydrates and thus always contain carbon, hydrogen, and oxygen, as do carbohydrates. In addition to these chemical elements, proteins always contain nitrogen and frequently also sulfur or phosphorus or both. The nitrogen, phosphorus, and sulfur in proteins are derived from the nitrates, phosphates, and sulfates absorbed from the soil. The chemical processes involved in the combination of sugar, nitrogen, phosphorus, and sulfur into proteins are among the most complex in plants and are only partly known. In the synthesis of proteins, the carbon, hydrogen, and oxygen derived from carbohydrates are combined in complex chemical reactions with nitrogen to form **amino-acids,** which may be regarded as the building blocks from which protein molecules are constructed. The amino-acid molecules become linked together in certain chemical reactions to form the large, complex molecules of proteins. Proteins are often stored as reserve foods in seeds (corn, beans, peas, soybeans). The chief function of proteins in living organisms is the construction of protoplasm, which is chiefly proteinaceous in nature. Proteins may also be used as sources of energy, but are much more commonly used to build protoplasm. The proteins stored in seeds are used chiefly in protoplasm formation in new cells when the seeds germinate.

Of the various food syntheses in plants, apparently only photosynthesis is directly dependent upon light. If sufficient quantities of sugars are present, protein and fat syntheses can usually proceed in unilluminated parts of plants.

Animals are able to convert carbohydrates into fats, and they are able to synthesize some proteins from amino-acids, which they can obtain only from green plants. Plants are sometimes called the "connecting link" between the inorganic and animal worlds, for they alone are able to convert inorganic materials into foods for both themselves and for animals. Green plants manufacture foods which support not only their own life processes, but those of all animals as well.

B. Methods of Getting Food

Plants which manufacture their own foods from simpler substances are called **autotrophic,** those which depend upon ready-made, externally supplied food are termed **heterotrophic.** Most important and most common of autotrophic plants are those which manufacture their foods by photosynthesis — in other words, all green plants. There are several species of bacteria which, though they lack chlorophyll, are able to manufacture foods by a process known as **chemosynthesis.** These bacteria, termed hydrogen, iron, nitrifying, and sulfur bacteria, oxidize respectively, hydrogen, certain types of iron compounds, ammonia, and hydrogen sulfide. These organisms obtain from these oxidation processes energy which they use in making foods from carbon dioxide and water. Since they utilize chemical energy rather than light energy, they are able to synthesize foods irrespective of the availability of light. The number of species of chemosynthetic plants is small as compared with that of photosynthetic plants.

There are likewise two main types of heterotrophic plants: **parasites and saprophytes.** Parasites are organisms which obtain their food directly from the living tissues of other organisms. Tapeworms, dodder, and many of the fungi which cause animal and plant diseases are examples of parasites. It might also be said that animals generally are parasitic upon the plant world. Some species of organisms are partial- or semi-parasites. Mistletoes, for example, contain chlorophyll and can therefore manufacture food; they cannot make enough food for themselves, however, and so supplement their diet by taking food away from the trees upon which they grow. Saprophytes are organisms such as bread-mold, Indian-pipe, most kinds of mushrooms, and puffballs which obtain their food from the dead bodies or waste products of living organisms, or from other non-living organic materials. Many species of very adaptable organisms can live either parasitically or saprophytically. Certain molds, such as the blue-green mold often found on oranges, behave as parasites when they attack the living tissues of their **host** (the organism which they parasitize) but later live saprophytically upon the dead tissues of the host. A few species of flowering plants, such as mistletoe, dodder, pine-drops, and cancer root, are heterotrophic.

The curious and unusual methods of obtaining supplementary food employed by insectivorous plants deserve mention again at this point in connection with the other methods by means of which plants make or acquire foods.

C. The Synthesis of Other Organic Compounds

Plants manufacture, in addition to carbohydrates, fats, and proteins, a great variety of other organic substances, such as chlorophyll, growth-regulators, anthocyanins, xanthophyll, carotin, suberin, vitamins, organic acids, etc. The significance to plants of some of these materials is unknown. In the case of others, such as chlorophyll, the importance of the compound in the physiology of plants is apparent. It should be remembered that many of the organic chemical compounds which are found in plants are waste materials, while others are substances with definite functions to perform.

Among the most important of the organic materials synthesized by plants are the **vitamins**. These are complex compounds most of which are synthesized only by plants. Although the chemical structure of some of the vitamins is known and the laboratory synthesis of certain vitamins is an accomplished fact, virtually nothing is known about the roles which these substances play in the metabolism of plants. They seem to be necessary for all normal plant growth and development, but their specific physiological actions are unknown. It has been suggested that they are involved in certain oxidation phenomena in plants and that they may be in some manner concerned in protein synthesis. Information concerning the importance of vitamins in the physiology of animals is much more extensive than that concerning their uses in plants. As every one who can read is aware, vitamins are necessary for the normal functioning of the human body and their deficiency leads to such serious disturbances as rickets, beri-beri, scurvy, loss of appetite, eye infections, nervous and mental disorders, etc. The inclusion in the diet of sufficient quantities of vitamin-containing foods such as butter, milk, cheese, eggs, fresh fruits and vegetables, fish oils, etc., corrects or prevents the above-mentioned deficiency diseases.

Most of the organic materials synthesized by plants contain hydrogen and oxygen, in addition to the carbon in their molecules, and frequently other elements such as nitrogen, magnesium, etc. Chlorophyll, for example, is composed of carbon, hydrogen, oxygen, nitrogen, and magnesium. All of these elements must be available in usable form and under proper conditions if chlorophyll is to be synthesized. Some of the substances such as iron and zinc, which are found in plants may be important in promoting certain physiological reactions without actually forming a portion of the products of such activities. For example, iron is not a constituent of chlorophyll, yet the synthesis of

chlorophyll by plants does not occur unless iron is present. A substance which influences chemical reactions in this manner without being incorporated into the products of such reactions is termed a **catalyst**.

D. ASSIMILATION

Assimilation might be termed the end result of many of these anabolic activities, for it is the process which converts individually nonliving foods, especially proteins, into living protoplasm and thus makes possible growth and reproduction. The actual physico-chemical processes involved in the conversion of foods into living substance are so intricate that little is known about them, except that proteins are the principal substances concerned and that considerable amounts of energy are required for these complex transformations.

2. CATABOLISM

The principal catabolic, or destructive processes which occur in living protoplasm are **digestion** and **respiration**. Most of the physiological activities of plants — assimilation, protein synthesis, digestion, respiration, etc. — occur in all living cells usually at all times so long as temperature, oxygen, and moisture conditions are favorable. Photosynthesis is most limited in extent and duration, since it takes place only in green cells and only when light is present. Anabolic and catabolic phases of metabolism usually proceed simultaneously in the same cell, for protein synthesis, assimilation, growth and certain other anabolic processes require considerable amounts of energy, which are furnished by the catabolic phases of metabolism.

A. DIGESTION

Digestion is the process whereby foods which are insoluble or very complex chemically are converted into foods which dissolve more readily in water or which are simpler chemically. Digestion is prerequisite to translocation, for only water-soluble foods can be moved from one part of a plant to other parts, and is also important as a preliminary to other processes, such as respiration, which ordinarily occur only when the foods involved in them are dissolved in water.

Digestion proceeds in virtually all living cells, but is especially active in the cells of tissues which store considerable quantities of foods. Thus, it is a conspicuous feature in most seeds, tubers, rhizomes, and other storage structures, particularly when they are beginning or resuming

growth after a dormant period. The principal kind of digestion which occurs in plants is **intracellular,** that is, it proceeds *within* the protoplasm cells. In some plants, such as many fungi and insectivores, digestive agents diffuse out of the cells, which produce them and thus act upon foods external to the cells in which they developed. This type of digestion, which is relatively infrequent in higher plants, is termed **extracellular.**

Digestion involves the uptake of water during the conversion of complex into simpler foods, as is shown by the formula representing the transformation of malt sugar to grape sugar.

$$C_{12}H_{22}O_{11} + H_2O \rightarrow 2C_6H_{12}O_6$$
(malt sugar)   (water)   (grape sugar)
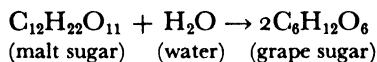
Thus, from the chemical standpoint, digestive processes are processes of **hydrolysis.** The mere addition of water to complex foods, however, is not sufficient to cause their transformation into simpler foods, for these complex substances are so stable that they require the action of catalysts to bring about their alteration.

These organic catalysts which are manufactured by living protoplasm and which promote the digestive and certain other processes of living organisms are called **enzymes.** There are many kinds of enzymes in plants; they vary in their speed of action, in the nature of the foods upon which they act, in their distribution in different parts and different species of plants, in their chemical constitution and in other respects. All of them have certain characteristics in common, however, of which the following are particularly conspicuous:

1. They are not used up in the processes which they promote.

2. They are highly specific in their action; that is, each enzyme usually catalyzes the digestion of a single kind of food, or sometimes several very similar kinds of foods. **Invertase,** for example, is an enzyme which acts upon cane sugar, **maltase** upon malt sugar, etc.

3. They are very sensitive to heat. Many of them are weakened or inactivated at temperatures of 160° F. and most of them are quickly destroyed by temperatures near the boiling point of water (212° F.).

4. They are complex colloidal materials, the exact chemical constitution of which is not known. Most of them appear to be proteinaceous substances.

5. They are highly efficient. Minute quantities of enzymes are able to digest large amounts of food in short periods of time. Many of the processes promoted by enzymes in living cells can be carried out in

test tubes using heat and strong acids in place of enzymes. Enzymes, however, are able to bring about such changes in living cells very easily, without the use of heat or acids, and thus are remarkably effective in the work which they perform.

The action of some, perhaps all, hydrolytic enzymes is reversible; that is, they not only convert complex foods into simpler ones, but they also under certain conditions build up the corresponding complex foods from the simpler types. The enzyme **maltase**, for example, digests maltose (malt sugar) into glucose (grape sugar) and is also able to synthesize maltose from glucose molecules. The reversible action of enzymes is very important in translocation and food storage. An insoluble food in one part of a plant may be digested by its particular enzyme into soluble foods; these may then be moved to some other portion of the plant and converted back into insoluble form by the same enzyme.

The hydrolytic activity of enzymes is affected by a number of environmental factors, such as temperature, acidity or alkalinity of the medium, light, the amount of the **substrate** (substance undergoing digestion) present, the presence or absence of accelerating or inhibiting substances, etc.

Enzymes are most frequently classified according to the substrates upon which they act and bear names which end usually in "*ase*." Among the common hydrolytic enzymes of plants are **amylase**, which converts starch into malt sugar, **invertase**, which digests cane sugar to grape sugar and fruit sugar, **lipases**, which digest fats into simpler substances (fatty acids and glycerin), **trypsin**, which transforms certain proteins into amino-acids, and other protein-digesting enzymes, such as **pepsins**, etc.

Enzymes, especially those of plant origin, are important in many industrial processes, in some of which the digestive action of living tissues is employed, in others of which the enzymes are extracted from the living cells and are then allowed to act dissociated from the protoplasm which produced them, upon certain substances of economic significance. The following list of uses made of enzymes attests to their great economic value: the preparation of sizing for textiles and paper, the removal (retting) of fibers from the stems of flax, hemp, and other plants, the degumming of silk, the preparation of skins for tanning, the manufacture of glycerin, the brewing and clarification of beer, the manufacture of alcohol, the clarification of syrups and pectin solutions, the making of bread, cheese, syrup from sweet potatoes, and

soy sauce, the ripening of tobacco, the fermentation of cacao (cocoa), the preparation of certain medicines (diastase and pepsin for digestive troubles, etc.), and the manufacture of various infant foods.

B. RESPIRATION

Respiration is the process whereby the energy stored in foods is released and made available for use by living organisms. Photosynthesis may be regarded as a process which converts the active energy of sunlight into the stored energy of foods; respiration is the activity which converts this stored energy into active energy available for assimilation, growth, movements, etc. Foods may thus be regarded as containers of energy or as the fuels which furnish the energy necessary for the operation of living machines. Respiration is chiefly a process of oxidation; that is, it involves usually the union of oxygen with the foods, usually sugars, undergoing respiration, as a result of which energy is liberated. The oxygen which is involved in the oxidative processes of respiration may be derived from free, atmospheric oxygen which enters the cells of plants dissolved in water, or it may be oxygen which is transferred from one type of chemical compound to another kind of compound. Respiration is frequently compared with the burning of wood or coal, which releases in the form of heat the energy stored in these materials. Obviously the comparison is a crude one, for oxidation in living organs proceeds at slower rates and at lower temperatures, and is subject to controlling factors unlike those involved in the burning of coal and wood. Of the energy released from foods by respiration, a portion escapes from the bodies of living organisms as heat, the remainder is used to provide the energy necessary for energy-using physiological processes, such as assimilation, growth, etc.

Respiration is sometimes defined as the intake of oxygen and the giving off of carbon dioxide by organisms, or is used synonymously with breathing. Such uses of the word "respiration" are confusing and, since they are erroneous, should be abandoned. Respiration is a *chemical* process which goes on in all living cells; the central feature of the process is the chemical reaction of oxidation, not the exchange of oxygen and carbon dioxide, which is merely incidental to the chemical process itself. The use of "respiration" in such terms as "artificial respiration" is inexcusable physiologically. The word which ·should be employed here is "breathing."

There are two main types of respiration: **aerobic respiration,** in which free, gaseous oxygen is available for the oxidation of foods, and

anaerobic respiration, in which little or no free oxygen is present for the respiration process.

In aerobic respiration, certain organic materials, chiefly sugars, are oxidized, with the result that energy is released and carbon dioxide and water are formed, as indicated in the formula

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + energy$$
(glucose) (oxygen) (carbon dioxide) (water)
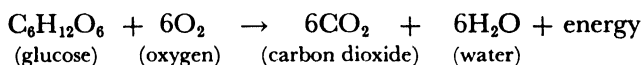
As stated earlier in this chapter, for every 180 grams of sugar made in photosynthesis, 674 calories of light energy are converted to the stored or potential energy of the sugar. In aerobic respiration, each 180 grams of sugar oxidized liberates approximately this same quantity of energy, as indicated in this formula:

180 grams $C_6H_{12}O_6$ + 192 grams $O_2 \rightarrow$
264 grams CO_2 + 108 grams H_2O + 674 calories
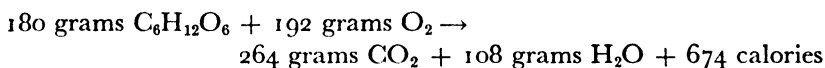
Glucose is the substance most commonly used in aerobic respiration. Other sugars are sometimes used, and less frequently fats, organic acids, proteins, and even protoplasm itself under conditions of extreme starvation. In certain bacteria, as described in the first part of this chapter, sulfur, hydrogen sulfide, iron compounds, ammonia, and other substances are the oxidizable substrates used in respiration.

The complex chemical changes involved in respiration are not completely known, nor is it known exactly how respiratory processes are controlled. The above formulae, then, are similar to that given for photosynthesis in that they represent only the initial substances and products of a long series of intermediate, imperfectly understood, complex chemical reactions. There are present in all living cells various kinds of **oxidizing enzymes** which in some plants have been shown to play important roles in respiration, particularly in anaerobic respiration. In addition, there is some evidence that iron, phosphorus and possibly other mineral elements are important controlling agents in respiratory processes.

The carbon dioxide formed in respiration diffuses out through stomata or lenticels into the external air, or a portion of it may be retained in the cells, in which it is formed and, if they are green, used immediately in photosynthesis. The water formed is retained within the tissues or evaporates from leaf or stem surfaces.

As stated above, respiration results in the production of heat, which is often easily measurable. In the development of the flower clusters in

certain species of tropical plants (aroids), the temperature of the flower cluster may be as much as 60° F. higher than the temperature of the surrounding air. Temperatures in masses of germinating seeds are frequently conspicuously higher than those of the outside air. If respiration proceeds rapidly in a poorly ventilated space, sufficient heat may be generated to cause a conflagration. For example, if incompletely dried hay is stored in large quantities in a tightly-walled barn loft, respiratory activity in any cells of the hay which are still living and in bacteria and other micro-organisms growing on the hay may develop enough heat so that the mass of hay bursts into flame. Frequently the burning of barns is attributable directly to this "spontaneous combustion," as it is popularly known. In some plants, such as certain species of fungi and mosses, a part of the energy released in respiration is used in producing a dim light known as **bioluminescence.**

There are many factors which influence the rate of respiration in plants — the amount of oxidizable material present, the acidity of the cell sap, the age of the respiring tissue, disease, the nature and quantities of enzymes present, temperature, injury, oxygen supply, carbon dioxide concentration, and others. A discussion of the effects of these many variables upon respiration is beyond the scope of this book.

Aerobic respiration may be regarded in a number of ways as the reverse of photosynthesis. The chief differences between these processes are shown in the table below:

Photosynthesis	*Aerobic Respiration*
1. Absorbs carbon dioxide and water	1. Liberates carbon dioxide and water
2. Liberates oxygen	2. Absorbs oxygen
3. Makes sugar	3. Destroys sugar (and other foods)
4. Increases weight	4. Decreases weight
5. Proceeds only in green cells	5. Proceeds in all living cells
6. Proceeds only in presence of light	6. Proceeds in the presence or absence of light

The gaseous exchange between green plants and the external atmosphere during the day is different from such exchange at night. During the day, both photosynthesis and respiration occur in leaves. Photosynthesis uses carbon dioxide and releases oxygen, whereas respiration uses oxygen and releases carbon dioxide. Photosynthesis proceeds more rapidly, however, than respiration, so that the carbon

dioxide produced in respiration is immediately used in green tissues in photosynthesis. The oxygen released in photosynthesis is in excess of that used by respiration, so a part of this oxygen escapes through the stomata and lenticels into the outer air. Thus, during the day, green plants give off oxygen and take in carbon dioxide. This makes it appear as though only photosynthesis were going on, for the gaseous exchange during the day is the characteristic gaseous exchange of photosynthesis. Actually, however, both photosynthesis and respiration occur during the day, but, so far as gaseous exchange is concerned, photosynthesis masks respiration because it goes on more rapidly. At night, photosynthesis ceases and respiration continues. Thus, at night, green plants give off carbon dioxide and take in oxygen, a condition exactly the reverse of that during the day.

Anaerobic respiration (fermentation), or incomplete respiration, makes use of many of the same foods which are respired aerobically, especially sugars, and to a lesser extent, fats, proteins, etc. In anaerobic respiration, no free oxygen is involved, and the energy release is achieved through molecular rearrangements in the substances undergoing this type of respiration. Carbon dioxide is one of the common products of anaerobic respiration. In addition to the carbon dioxide, some other product, usually ethyl alcohol or some organic acid as lactic acid (in sour milk) or butyric acid (in rancid butter) is produced, together with the release of energy. These organic products are usually capable of further decomposition in the presence of free oxygen, with the release of further supplies of energy and the formation of carbon dioxide and water. Anaerobic respiration is frequently called **incomplete respiration** for this reason; if gaseous oxygen is available, the products of anaerobic respiration may be oxidized completely to carbon dioxide and water.

The best-known example of anaerobic respiration is the **alcoholic fermentation** of sugar by yeasts, which are minute, one-celled fungi. In yeasts, if the oxygen supply is limited, sugar is respired anaerobically, as a result of which some energy is released and carbon dioxide and ethyl alcohol are formed. If abundant oxygen is available, most yeasts continue their respiration aerobically and the alcohol is oxidized completely to carbon dioxide and water, with the release of additional amounts of energy. Acetic acid bacteria, which are often present on the skin of grapes and other fruit, in the presence of small amounts of oxygen are able to convert the ethyl alcohol formed by yeast into acetic acid and water. Acetic acid has a very sour taste, responsible for the

sour flavor of vinegar and of wine in which acetic acid bacteria have been at work. This conversion of alcohol to acetic acid by these bacteria is termed acetic acid fermentation.

It is believed by many physiologists that anaerobic respiration occurs in all living cells. In many lower types of organisms, such as certain yeasts, molds, bacteria, and other fungi, anaerobic respiration is the only type of respiration normally carried on, and these organisms frequently will live only in the absence of free oxygen. Most higher plants respire anaerobically for a time at least, if they are deprived of oxygen. There is evidence for the belief that in higher plants respiration occurs in two stages — first, an anaerobic phase, like the anaerobic respiration of yeasts, etc., followed by an aerobic phase in which the products of the anaerobic stage are completely oxidized to water and carbon dioxide. Many kinds of fungi are exclusively anaerobic in their habit of life and in their respiration. Although higher plants also respire anaerobically, they can live normally only in the presence of oxygen and thus they complete the process of respiration, oxidizing completely the products of the anaerobic phase of respiration to carbon dioxide and water.

Anaerobic respiration is important to man in several ways. The manufacture of alcohol, alcoholic beverages, and vinegar, the spoilage of many types of foods, the manufacture of cheese and other kinds of dairy products and of sauerkraut, and the preparation of ensilage in silos are the results of processes of anaerobic respiration by micro-organisms. Much of the decomposition of dead bodies of plants and animals in the soil and of their waste products is attributable to the anaerobic respiration of these materials by certain anaerobic bacteria and other fungi. These processes of decomposition result in the ultimate restoration to the soil and the air of the simple substances which were tied up in the complex organic constituents of plant and animal bodies and their waste products.

It should be emphasized that, although many micro-organisms produce in their anaerobic respiration substances important to man, these substances are merely waste products so far as these organisms are concerned. Anaerobic respiration is important to these plants because it furnishes them with energy; the possible use by man of the waste products of this respiration is incidental to them. Yeasts, bacteria, and other fungi are usually inhibited or destroyed by the accumulation about them of their waste products; yeasts, for example, are injured when the concentration of alcohol surrounding them reaches 15 per cent.

SUMMARY

1. Metabolism is the sum total of all chemical transformations which occur within living protoplasm.

2. The term "anabolism" refers to those metabolic processes which can occur only when energy is supplied to them and which result in the building-up of complex organic substances and protoplasm, e.g., photosynthesis, assimilation. "Catabolism" refers to those processes which tear down organic substances and protoplasm and which release energy.

3. A food is an organic substance which furnishes energy or is used in the construction of protoplasm.

4. The three principal types of foods are carbohydrates, fats, and proteins.

5. Carbohydrates supply energy, build cell walls, and are the fundamental substances from which fats, proteins, and other substances are synthesized.

6. Fats are chiefly storage foods and constituents of protoplasm. They are able to release more energy than are carbohydrates when they are respired.

7. Proteins are the chief constituents of living protoplasm. They may also be used as sources of energy.

8. Green plants require, in addition to carbon dioxide and water, nitrogen, phosphorus, sulfur, and other elements which are absorbed from the soil and used in various synthetic processes.

9. Green plants can be successfully grown in properly balanced water solutions of minerals.

10. Autotrophic plants are able to manufacture their own food. Most autotrophic plants have chlorophyll and carry on photosynthesis. Some autotrophic plants (some bacteria) manufacture foods using energy obtained from chemical oxidations; such processes of food manufacture are called chemosynthetic.

11. Heterotrophic plants are unable to manufacture their own food and live as parasites, obtaining their food directly from the tissues of some other living plant, or saprophytes, obtaining their food from dead or non-living organic matter.

12. Vitamins are among the many substances synthesized by plants. Their exact roles in plant metabolism are not known.

13. Assimilation is the conversion of foods, which are non-living, into living protoplasm.

14. Digestion is the conversion of insoluble or complex foods into soluble or simpler foods.

15. Digestion is brought about largely through the action of digestive agents, called enzymes. Digestion processes belong to a type of chemical reaction known as hydrolysis, in which water is used in the reaction.

16. Enzymes are organic catalysts. They are manufactured by living protoplasm, are highly specific in their action, are not used up in the processes which they control; they are highly efficient, being effective in very small quantities, and they are destroyed by heat.

17. Respiration is the process whereby the energy stored in foods is released and made available for use by living organisms. Respiration is chemically a process of oxidation.

18. Aerobic respiration proceeds in the presence of abundant free, atmospheric oxygen. This formula represents the reacting substances and products in a common type of aerobic respiration:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$$
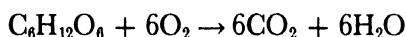
Anaerobic respiration (fermentation) proceeds in the absence of free oxygen or in its limited presence. The substances most commonly respired by plants are sugars.

19. Many organisms, especially certain fungi, are able to respire only anaerobically. Most plants seem to have two phases in their respiration — first, an anaerobic, followed by an aerobic phase.

20. Fermentation processes are of great importance in industry and agriculture.

21. Part of the energy released in respiration is used in assimilation, growth, and other endothermic activities, some is released as heat.

Growth and Irritability

1. THE NATURE OF GROWTH

THE WORD "growth" usually signifies to the lay-
man increase in size. To biologists, however,
growth is an infinitely complicated phenomenon, with many more
implications than mere enlargement. In the biological interpretation
of growth, three fairly distinct phases are recognized: first, the forma-
tion of new cells by the processes of mitosis and cell division; second,
the enlargement of the newly-formed cells; and third, the differenti-
ation, or maturation, of these enlarging cells into the mature tissues of
a growing organ. There are no sharp lines of demarcation among these
stages of growth, each phase merging gradually into the next. The terms
"cell formation," "cell enlargement," and "cell differentiation" refer to
characteristic stages in a continuous process. Thus, increase in size is but
one phase of growth. Equally important in the growth of living organ-
isms are the co-ordination of physiological activities and the subordi-
nation of these activities to the growth plan of each species, whereby
differentiation and the orderly development of tissues and organs occur.
Growth without co-ordination results in **hypertrophy** — the formation
of abnormal growths, such as plant tumors, galls, etc. Various internal
maladjustments and external conditions such as insect or fungous at-
tacks interrupt the normal procession of these growth phases and thus
cause such abnormalities to appear.

Growth may be considered in a broad sense as the result of an excess
of anabolic activity over catabolic processes. Anabolic processes result
in an increase in protoplasm, a fundamental feature of plant growth,
whereas catabolic activities simultaneously bring about a decrease in
organic protoplasmic constituents. So long as anabolism proceeds in
excess of catabolism, the synthesis of protoplasm and of cell wall
materials outweighs their destruction, and growth occurs. If, through
unfavorable environmental conditions or old age or disease, catabolic

activity exceeds anabolism, then protoplasmic constituents are torn down more rapidly than they can be synthesized. Under such conditions growth ceases, and there may result a decrease in the volume and weight of protoplasm and of the organic materials which make growth possible. Thus, growth involves important nutritional relationships; only when there are sufficient quantities of amino-acids and proteins for protoplasm and when there are respirable materials such

Fig. 120. Stages in development of a cell
    A. Embryonic cell.
    B. Young, growing cell.
    C. Mature cell.

        a. cell walls.
        b. cytoplasm.
        c. vacuoles.
        d. nucleus.
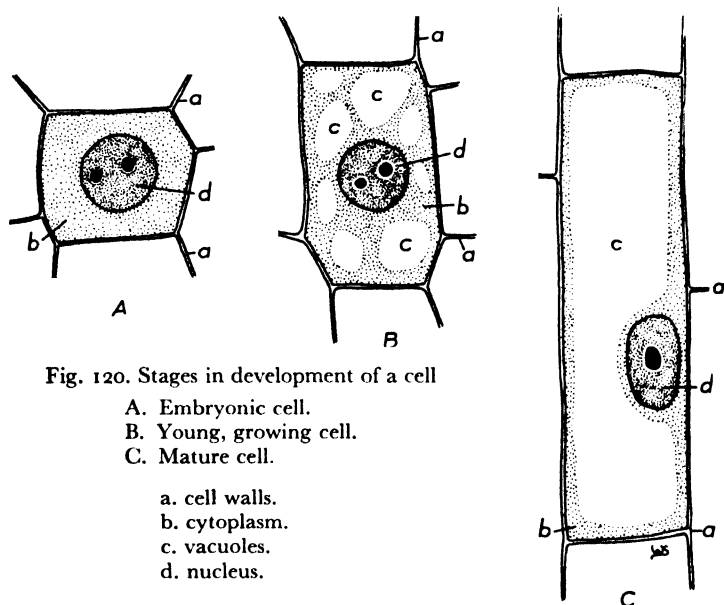
as carbohydrates to furnish energy for the endothermic protoplasm-building activities can normal growth occur.

The rate at which growth occurs varies in different species, as stated in Chapter III, and also through three growth phases, if growth is measured in terms of increase in size, as is customarily done. Growth begins slowly, then enters upon a period of rapid enlargement, following which it gradually decreases until no further enlargement occurs. The mathematical curve which represents this variation in growth rate is thus an S-shaped curve. Growth, as stated above, is most frequently measured in terms of increase in volume, length, area, or dry weight, depending upon the nature of the plant or organ in which growth is being studied. Most indicative of the growth efficiency of a plant is doubtless dry weight increase. Though biologists are constantly aware

that differentiation is an important stage of growth, they possess no satisfactory method of measuring quantitatively the rate or degree of differentiation. Quantitative techniques are applicable chiefly to the enlargement phase of the growth process.

Embryonic cells are usually small, cubical or nearly so in form, thin-walled, and packed with dense cytoplasm in which the vacuoles are very small and inconspicuous. The embryonic, or meristematic, cells of cambium layers are usually elongated, rather than cubic in form, though they are like all other types of embryonic cells in their possession of dense, physiologically active protoplasm. The formation of new cells from embryonic cells in the growth processes of most plants involves the process of mitosis. Whenever a meristematic cell divides, its nucleus is divided into two new nuclei by mitosis, so that each of the two daughter cells which arises from the division of a parent cell contains its own nucleus with the same hereditary potentialities as those of the parent nucleus. Newly-formed cells enlarge rapidly, with marked lengthening of their cell walls, an increase in the amount of protoplasm present, and usually a coalescence of the small vacuoles characteristic of the embryonic cells, into a single, large central vacuole (Figure 120). In the final stage, differentiation, cell walls are thickened, and the various sculpturings, pits, etc. appear in them. The differentiation phase marks the fixity of middle-age, beyond which no further enlargement of cells occurs.

Growth does not simultaneously occur in all parts of plants, but as indicated in earlier chapters, proceeds chiefly in certain tissues, known as meristematic, or embryonic tissues. These are normally the growing points of the tips of roots and the buds of stems, the cambium, cork cambium, and root pericycle. In many plants, certain differentiated cells, particularly parenchymatous cells, occasionally undergo a process of dedifferentiation, that is, they are transformed from matured cells into meristematic cells and are capable of growth and the production of adventitious roots, buds, etc. In all of these growing parts of plants, the same sequence and pattern of growth-phases occur — cell formation, cell enlargement, and cell differentiation. These phases may be observed in microscopic preparations of root tips, buds, cambial regions, etc.

Growth is the product of a number of physiological processes and may thus be regarded as the culmination of all metabolic activities. It involves the absorption of water and of minerals, the manufacture of food, the digestion, translocation, and assimilation of food, the re-

lease of energy needed for assimilation and other growth phases by the process of respiration, the construction of cell walls from pectic substances and cellulose, the intricacies of mitosis, etc.

As a complex of other processes, growth is not capable of simple definition, but can be defined adequately only on the basis of the stages or phases, of which it is constituted. The most satisfactory attempt at a forthright definition of growth states that it is a more or less irreversible change in the structure or development of a cell, tissue, organ, or organism.

Since growth is a resultant of numerous physiological processes, it is affected by the diverse internal and external factors which influence these metabolic activities. These factors will be considered briefly in the next two sections of this chapter.

2. THE INTERNAL FACTORS WHICH INFLUENCE GROWTH

The internal factors which affect growth are chiefly those inherent in the protoplasm of a species (hereditary factors), or which have been previously induced in the protoplasm by external features of the environment. It is not always possible to distinguish easily between internal and external factors; for example, the amount of food stored in the roots of a perennial plant is an important internal factor in determining in large part the features of the next season's growth. The food thus stored, however, depended upon the amounts of water, light, carbon dioxide, etc. available at the time when it was synthesized in the preceding growing season.

The hereditary potentialities of individual species of plants are important internal factors which regulate growth. Some species of trees such as poplars and willows, grow very rapidly in the presence of favorable external conditions; pines, white oaks, and sweet gums exposed to similarly advantageous conditions grow much more slowly. Morning-glories are by nature twining vines with weak stems, and although their rate of growth may be markedly influenced by variations in their external environment, they always remain weak-stemmed twiners. The buds of honey-locust trees produce leaves which are pinnately compound; the rate of growth of such leaves is subject to environmental variations, but the compound nature of the leaves cannot be changed by alterations in moisture, temperature, etc. The time of flowering of tobacco plants may be shifted by changes in the daily

duration of light to which they are exposed, but the plants always remain recognizably tobacco plants, with the traits and potentialities of the tobacco species. Thus, variations in environmental factors can induce certain changes in gross structure, anatomical features, reproductive phases, etc., but the degree and quality of these changes are limited in the final analysis by that most important internal controller — the hereditary constitution of the species. Such a constitution is always liable to amendment, but never to fundamental change.

Growth regulators, or **auxins** (sometimes termed "plant growth hormones") constitute another of the important internal mechanisms which regulate growth. Auxins are, chemically, organic acids which are manufactured by the protoplasm of many kinds of living plant cells. They are especially abundant in growing parts of plants — buds, root tips, cambium cells, etc. — and they exert far-reaching effects upon various growth phenomena. They regulate the elongation of cell walls and are thus of tremendous significance in cell enlargement, they influence root production and the activity of cambium, they frequently inhibit the development of certain buds and hasten the growth of others, and they apparently constitute the mechanism whereby excitations set up by external stimuli are transmitted from one portion of a plant to other parts.

Certain of these growth-promoting substances from plant tissues, as well as a number of chemically related substances have found extensive commercial use in horticultural and agricultural practices. Liquid and powder preparations of some organic acids, such as indole-acetic and indole-butyric, are used by gardeners and nurserymen to promote the rapid formation of roots on cuttings of many kinds of shrubs and trees; not only do these preparations accelerate the rate of production and growth of roots on cuttings but they induce the development of roots in the cuttings of some species which under normal conditions do not form adventitious roots. Growth-regulating substances also stimulate the enlargement of the fruits of various plant species (e.g., cotton, watermelon) without pollination and the production of seeds. Certain growth regulators, sprayed on developing fruits (e.g., apples) prevent the falling of fruit, so that the number of windfalls is greatly reduced. This is a treatment of great commercial value, for fruits which are picked from trees do not have the bruises and partly rotten tissues which greatly reduce the value of windfalls.

Vitamins are substances which are synthesized by plants and which seem to be present in all plant cells. Little information exists concerning

their importance in the metabolism of plants, but as stated in the preceding chapter they are known to influence markedly many physiological processes and developmental phases in animals and probably in plants as well.

Other examples of internal regulation of growth in plants are found in the phenomena of **correlation,** the mutual interaction of parts. Physiological changes in one part of a plant frequently affect the development of other portions of a plant body. For example, if a whole potato tuber is planted, only the buds at the terminal end form sprouts. If the tuber is cut into three or four segments, all of the buds on all segments begin to grow. The terminal buds of potato tubers and of many other kinds of stems form growth-regulating substances which diffuse basally and inhibit the growth of some of the axillary buds. When the passage of these inhibitors is interrupted by the sectioning of the tuber, the axillary buds are freed from the effects of these substances and are able to grow. Another common example of correlation is that between vegetative and reproductive processes. In many kinds of plants, such as sweet peas and pansies, the daily removal of flowers promotes continued growth and blossoming; if flowers are allowed to remain on the plants, however, they develop into fruits, and further growth and flower-formation cease, for fruit production draws heavily on the food reserves of plants and frequently results in death. In century plants (*Agave*), vegetative growth continues for many years, until large quantities of food are stored within their tissues; when these reserves of food reach a certain abundance, the plants form flower stalks of tremendous size. The production of these flower clusters and the subsequent formation of fruits constitute such a tremendous drain on the reserve foods that the plants die as result of their procreative activities. Correlations of many types can be explained on the basis of auxin secretion and activity; in other cases, as in the correlation between reproductive and vegetative processes nutritional relationships are the most obvious controlling factors, although auxins may also be involved. In certain types of correlation, satisfactory explanations are wanting.

Another important internal growth factor is age. Young cells, tissues, and organs generally grow more rapidly under similar environmental conditions than do older parts of plants. As stated earlier in the chapter, mature tissues may become "dedifferentiated" and resume such growth as is characteristic of young tissues and organs. The variations in growth rate at different ages are attributable partly to

alterations in the production and effectiveness of auxins at these different stages.

The ratio between carbohydrate and nitrogen compounds in plants is partly an internal, partly an external factor which may determine in many plants whether vegetative or reproductive activities are to predominate. In some species of plants, such as tomatoes, an excess of nitrogen appears to prolong vegetative growth and delay reproduction. A marked reduction in available nitrogen and a concomitant increase in carbohydrate synthesis frequently results in stunted vegetative growth and acceleration of reproductive activity. If a suitable balance is maintained between available nitrogen and carbohydrate synthesis, both vegetative and reproductive activities may be promoted. Thus, the carbohydrate-nitrogen ratio is perhaps an important factor in controlling vegetative growth and reproduction in some species of plants. In other species, a change in the carbohydrate-nitrogen ratio is a result, not a cause, of the shift from a vegetative to a reproductive condition.

3. THE EXTERNAL FACTORS WHICH INFLUENCE GROWTH

The principal external factors which affect growth and configuration of plants are *light and other types of radiations, temperature, moisture, mineral nutrients, foods, oxygen, carbon dioxide, and other gases, anesthetics, poisons, gravity, mechanical factors such as pressure and contact, the attacks of parasites,* and others. A noteworthy feature of this list is the fact that most of these environmental conditions, which influence plant growth, likewise exert profound effects upon the development of animals. The susceptibility of all living organisms to the same features of their environments is another indication of the fundamental unity of all living protoplasm.

It should be emphasized again that it is exceedingly difficult to delimit sharply external from internal factors, for external factors are able to influence the growth and development of organisms only through their effects upon these internal processes. Many external influences of widely different nature affect certain internal factors similarly and thus induce similar growth and configurational changes in organisms.

These diverse factors of the external environment affect plants in one or more of four ways; they influence the rate of growth of their

tissues, they exert influences upon the form and structure of certain organs (limited, of course, by the internal organization of each species), they affect reproductive activity, and if they act in different intensity from different directions, they frequently induce movements (responses, or reactions) of various plant organs.

In this section of the chapter, the effects of certain of these influences upon plant growth and form will be briefly discussed. The movements of plant organs in response to directional differences in these various factors will be described in the second half of the chapter as a phase of irritability. It is impossible in an elementary textbook to discuss the growth effects of all of these environmental features; thus, only the most striking influences of these stimuli will be considered.

The sole source of energy for green plants is the radiant energy from the sun. The visible portion of this radiation, called *light*, is most significant in the lives of plants. Light influences the germination of certain kinds of seeds, the rate of photosynthesis in leaves, the anatomical structure of leaves, the rate of growth of various organs, the initiation of reproductive processes, the external forms and sizes of stems and leaves, and many other features of plant growth. One of the striking effects of light is the reduction which it causes in the rate of elongation of stems. Light affects the growth rate and form of plants largely through its relation to photosynthesis, which operates only in the presence of light. The rate of growth and to a certain extent the size and form of organs depend directly upon the kinds and amounts of foods available for the construction of new protoplasm and for energy release. Thus, through photosynthesis, light influences a variety of other metabolic activities. Light also exerts direct effects upon other processes in plants — upon the decomposition and synthesis of chlorophyll, upon enzyme functions, upon auxin production and activity, upon the physico-chemical condition of certain protoplasmic proteins, upon the opening of stomata, etc. Plants which grow in the dark show **etiolation,** a condition characterized by abnormally elongated, weak, spindly stems, undeveloped leaves, and pale, yellowish, chlorophyll-less tissues. Only when they receive adequate supplies of light do plants develop in normal fashion. Excessive intensities of light frequently stunt somewhat the growth of plants, largely as a result of the effects of such intensities upon the transpiration, enzyme activity, the stability of proteins in the protoplasm, the production of growth substances and other processes. Plants grown in diffuse light are usually larger, with more succulent leaves than those growing in full sunlight. Several species of crop

plants such as tobacco and lettuce are frequently cultivated under cheesecloth screens to produce larger or more succulent leaves. The duration of daily exposure to light is also a factor which influences the growth of plants particularly with respect to the onset of their reproductive phases. Certain species which blossom during early spring or late summer when the days are short are termed **short-day** plants; examples of such plants are asters, tobacco, certain soybean varieties, and cosmos; **long-day** plants, such as lettuce, goldenrod, and certain soybean varieties, blossom only when the length of daily exposure to light is more than twelve hours. Other species, such as tomato, are seemingly independent of variations in daily light duration and flower both under short-day and long-day conditions. Studies on the flowering responses of plants with respect to day length have led to many practical results in the culture of various greenhouse crops. By decreasing day length by shading plants during certain hours or increasing it by means of supplementary electric illumination at night, horticulturists are able to control the blossoming and fruiting time of many species of greenhouse plants.

Growing plants are constantly influenced by variations in the temperature of the soil in which they grow and of the surrounding air. Most species of plants in active condition develop best in temperatures between 70 and 90° F. and cease growth when air and soil temperatures approach freezing or rise much above 100° F. Dormant (relatively inactive or resting) structures, such as seeds or spores, with low water content are much more resistant to extremes of temperature than are actively growing organs. Seeds and spores have been known to endure, without apparent injury or loss in their germinating ability, temperatures as low as − 266° F. for six months and for shorter periods as high as 220° F. (above the boiling point of water). The active cells of certain bacteria and blue-green algae, which grow in water from hot springs, thrive at temperatures not far below the boiling point of water, a condition unusual for cells other than those in dormant condition. The maximum, minimum, and optimum (best) temperatures for seed germination and plant growth vary of course with different species of plants, with age, with other environmental conditions simultaneously operative, etc. Barley seeds, for example, germinate and grow at temperatures only slightly above the freezing point of water, corn seeds usually will begin their growth and activities only if the temperature of the soil is about 50° F. or higher, and the seeds of cucumbers and other members of their family do not sprout unless soil

temperatures are above 55° F. Aside from its effects upon the rate of growth, temperature influences plants in many other ways. Very low and rather high temperatures shorten the rest period of many dormant structures such as seeds, corms, tubers, etc. Temperatures also exert an influence on the carbohydrate-nitrogen ratio of plants and thus are frequently important in the balance between vegetative and reproductive phases. Temperatures near 32° F. cause injury to and often kill the tissues of many plants; some plants, such as alfalfa and cabbage, for example, can be **hardened** to temperatures near freezing, if they are sprouted from seeds at higher temperatures and are then exposed gradually to successively lower temperature. Such hardened plants are less susceptible to injury when air temperatures fall almost to the freezing point. Temperature affects plant growth and form chiefly through its effects upon the various physical and chemical processes which occur in plants; diffusion, enzyme action, photosynthesis, respiration, etc. proceed more rapidly as the temperature rises, until it reaches a point at which heat damage to protoplasm occurs.

The importance of water in the life of plants has been considered in an earlier chapter. The relation of plants to water is a very complex one and involves problems of osmosis, water transport, transpiration in relation to water absorption by roots and in relation to wilting, atmospheric conditions, etc. The amounts of water available to plants influence markedly their growth and form. Since water is one of the raw materials of photosynthesis, its availability is related to the quantities of food manufactured in plants. The growth of cell walls and the formation of new protoplasm depend directly upon the amount of food formed in photosynthesis. Chiefly through its effects upon these processes and upon the turgor of cells, the water supply of plants influences growth rate and the ultimate size attained by various tissues and organs. If transpiration becomes excessive, the amounts of water available for food synthesis and for the turgor pressure required for cell-wall stretching are limited, and growth is correspondingly diminished. With reduced transpiration, growth is more rapid and plants generally attain larger sizes as a result of the greater quantities of water at their disposal. Most species of plants possess minimum, maximum, and optimum soil moisure concentrations which influence their growth. Plants may be stunted in their development by too much water as well as by too little. In mesophytes, a scarcity of water results in stunted growth because of reduced food synthesis and assimilation; an excess of water in the soil may likewise stunt growth through the exclusion

of oxygen necessary for root development; growth is best promoted by moderate supplies of water which are sufficient for rapid food manufacture and assimilation and yet do not exclude oxygen from the soil. Different species of plants are diversely adjusted to moisture conditions of their environments. Water lilies grow only where their roots are submerged in water, forget-me-nots require continually damp but not saturated soil for their growth, whereas cactus plants quickly rot unless the soil in which they are rooted is rather dry most of the time. In addition to its effect upon the rate of growth, water supply frequently exerts a direct influence upon specific morphological features of plants. For example, the roots of corn plants grown in water cultures do not produce root hairs; in damp soil or in saturated air, root hairs develop in great abundance. The structural differences among xerophytes, mesophytes, and hydrophytes are often in large degree expressions of the relations of moisture to their growth.

The quantities and kinds of mineral salts available to plants exert tremendous influence upon growth, for the failure of plants to obtain the elements necessary for food syntheses, chlorophyll formation, etc., results in pronounced metabolic aberrations. If nitrogen is not present in sufficient quantities, growth is poor, because nitrogen is a constituent of proteins, of chlorophyll, and of other organic compounds required for assimilation, food manufacture, etc. The absence of iron and magnesium from the soil prevents the development in plants of chlorophyll. Sulfur and phosphorus are necessary in the elaboration of some proteins and their scarcity is reflected in the failure of normal protoplasmic development and functioning. The presence of certain minerals in a soil may render other minerals unavailable to plants, as a result of which the plants growing in such soils show deficiency symptoms. For example, in Hawaii, pineapple plants frequently suffer **chlorosis,** a condition characterized by poor chlorophyll development, because iron in the soil is rendered unavailable by excessive quantities of manganese in the soil. This chlorosis may be remedied by spraying iron-sulfate solution on the pineapple leaves, which are able to absorb sufficient amounts of iron from this solution to develop normal quantities of chlorophyll.

Oxygen is required for normal root growth and for respiration, and its absence is soon indicated by abnormalities in growth. Carbon dioxide is a raw material of photosynthesis and hence its presence is necessary for the manufacture of carbohydrates. A moderate increase in the carbon dioxide content of air usually accelerates photosynthetic

Photo by Missouri Botanical Garden

Fig. 121. *Cineraria* plant showing injury from sulfur dioxide in smoke.

activity. If the percentage of atmospheric or soil carbon dioxide becomes excessive, plants may be injured as a result. Other gases influencing plant growth are the gases, such as sulfur dioxide, which escape into the air from smelters, factories, etc., often as products of the combustion of coal and of other materials involved in industrial activities. These gases frequently cause serious injury to plant tissues (Figure 121) and often kill various species of plants, particularly evergreens which are more susceptible than most other plants to such injury because they retain their leaves during the winter, when the smoke and gas content of the air near congested industrial centers is highest. Plants are exceedingly susceptible to small traces of illuminating gas. Concentrations of one part of illuminating gas in 40,000 parts of air kill the buds of carnations and 50 parts of such gas in a million parts of air are sufficient to cause the petals of tomato flowers to show abnormal bendings. These concentrations are so low that the gas does not affect the human sense of smell. One of the reasons for the poor growth of many kinds of plants in houses is the presence in the air of minute amounts of illuminating gas escaping from stoves and other gas connections. These traces of gas are so small that they are harmless to human beings, but they stunt the growth of plants, cause the premature fall of leaves, etc.

Many types of chemical compounds, such as those of mercury, arsenic, silver, etc., alcohol, etc., are very poisonous to plants and quickly kill them if they are present in the soil or the air surrounding the plants.

External factors such as pressure and contact affect plant growth and form chiefly through their mechanical effects. Contact sometimes exerts a specific morphological influence in plant growths; the tendrils of Boston ivy, for instance, have very slender tips which remain slender in the absence of contact; if they touch solid objects, the tips are quickly

transformed into disc-shaped cushions of tissue which anchor the tendrils very tightly to the object which furnished the stimulus.

Parasites such as fungi, insects, worms, etc., affect plant growth in various ways. The attacks of some fungi, such as that which causes the club-root disease of cabbage, and many insects result in the formation of hypertrophies such as tumors, galls, and other types of abnormal swellings.

4. IRRITABILITY AND STIMULI

Irritability, one of the most characteristic properties of living protoplasm, is a two-fold phenomenon involving first, sensitivity to stimuli, and second, reaction or response to these stimuli. The stimuli which induce the movements or reactions of plants are principally those mentioned in the first section of this chapter — light, water, contact, gravity, gases, etc. When these external factors are diffuse or when they are more or less equally distributed about a plant, their usual effects are upon growth rates and form, as described in the preceding section. If, however, these stimuli are concentrated in certain parts of the environment and are thus more powerful on one side of a plant organ than on another, they affect growth rates and other physiological activities very unequally in various parts of the growing organs. As a result, changes in position of the organs subjected to such stimuli are brought about. Reactions in which an organ moves toward the source of the stimulus are termed **positive,** those which result in movement away from a stimulus are called **negative** reactions. These plant reactions or movements are usually too slow to be observed by the human eye but that they actually occur can be demonstrated by time-lapse motion picture photography or, more simply, by observing reacting plants at intervals of several hours and noting changes in position of the various organs. All kinds of plants exhibit reactions to environmental stimuli. The reactions of plants differ in their speed, direction of movement, the nature of the mechanisms which bring them about, and in other respects. Despite the many variations among the diverse kinds of plant movements, there are certain features common to most kinds of reactions, chief among which are reception of stimuli, the transmission of **excitation** (the irritation set up in a living tissue by a stimulus), and the changes in certain cells or tissues which actually bring about a reaction or movement. Through their responses plants become adjusted to their environments.

5. RECEPTION OF STIMULI BY PLANTS

Only those stimuli which plants can receive — that is, which induce protoplasmic irritation — initiate reactions. Light, temperature, moisture, mineral salts, for example, are stimuli which affect the protoplasm of plants; musical sounds, on the contrary, do not stimulate plant protoplasm and thus do not induce reactions.

The reception of stimuli by plants is frequently compared with the reception of warmth and cold by human skin; that is, there are no morphologically differentiated receptive structures in most plants and the reception of external stimuli is therefore somewhat diffuse in many parts of plant bodies. Generally all portions of leaf blades are sensitive to light, and all plant organs are sensitive to temperature changes, to moisture, and to many other stimuli. In certain cases, there are definitely localized groups of cells which act as sensory or perceptive zones. In most roots, for example, certain cells are apparently more effective than other root cells in detecting the stimulus of gravity, if roots are placed in a horizontal position. Intact roots in such a position soon begin to turn downward, but if their tips are cut off before the roots are placed on their sides, no bending occurs until a new root tip is regenerated. This behavior indicates that in many plants reception of the stimulus of gravitational force by roots is limited to these special root tip cells. Similarly, in many kinds of plants, the stimulus of light is received more readily by certain groups of cells than by other cells. In the seedlings of grasses, such as oats and corn, only the tip of the young sheath, which encloses and protects the young leaves, receives effectively the stimulus of light. If this tip is cut off or shaded and only the cells below the tip are exposed to light, little or no bending of the sheath occurs. If the tip is illuminated, however, the stimulus is received and a strong bending toward the light results. In the leaves of the Venus'-flytrap, only the sensory hairs on the inner surfaces of the leaves are able to receive contact stimuli; all other parts of the leaves are insensitive to such stimulation. Thus, in some plants, there are somewhat localized or specialized sensory zones or regions, as described above. Usually, these sensory zones are not highly specialized morphologically except in such cases as the sensory hairs of the flytrap, but differ chiefly in a physiological manner from the other cells surrounding them. In the majority of plant responses, however, such localized sensory areas are not demonstrable; reception, then, is largely diffuse in plants, and aside from such cases as those described above, takes place in many cells of plant bodies.

6. THE TRANSMISSION OF EXCITATION

As already explained, the irritation which is set up in living cells by stimuli is usually termed **excitation**. A common feature of most plant reactions (as well as of animal reactions) is the fact that the reception of stimuli frequently occurs in one part of an organ, while the actual bending which is induced by the stimulus is executed in another part of the excited organ. Thus, there must be a transmission of excitation from the place in which it is initiated by the external stimulus to the region of reaction. In higher animals, nerves constitute the machinery of such transmission. No such structurally specialized tissues for conducting excitation occur in plants. It has been demonstrated in recent years that auxins and other regulatory chemical compounds are responsible in large part for the protoplasmic transmission of excitation in plants. Various external stimuli influence the production, rate of movement, distribution, and effectiveness of auxins in growth processes. As a result largely of unequal distribution of these auxins, occasioned by certain external stimuli, differences in rates of growth occur in different parts of organs and, as a result, bending of the organs occurs. Plasmodesmata, the protoplasmic strands which connect the protoplasts of adjoining cells, apparently facilitate the movement of auxins. Auxins are able to travel by diffusion through walls and by passage through plasmodesmata from one living cell to another. They also move through the conducting elements of the xylem and likewise through sieve tubes of the phloem.

Thus, transmission of excitation in plants is achieved largely by means of the passage of chemical agents from cell to cell or organ to organ as contrasted with the transmission in animals, which is largely through morphologically specialized nerve systems.

7. THE KINDS OF REACTIONS IN PLANTS

The reactions or movements of animal bodies and parts of animal bodies are the results of muscular contraction and relaxation. In plants, which lack such contractile tissues, the actual mechanism of movement is most commonly an inequality in the rates of growth of different tissues, or less frequently, a change in the turgor (water pressure) in certain tissues. The main types of plant movements are classified principally upon the basis of the actual internal mechanism which brings about the reaction.

Fig. 122. Left. Positive phototropism in geranium; notice that the stems and petioles have turned toward the source of illumination at the upper left.
Right. Leaf-mosaic of geranium, a result of phototropic bendings of the petioles.

Most common and most significant of all plant movements are **tropisms.** These are bending movements of cylindrical organs, such as petioles, stems, roots, flower stalks, etc., in response to certain external stimuli. Tropisms are common throughout the plant kingdom; they occur in many fungi, in bryophytes, in ferns, and in seed plants. The cause of the bending of organs of the type described above is a difference in rate of growth in different parts of the reacting organs. One side grows more rapidly than another side, as a result of which the more rapidly growing side becomes convex, the less rapidly growing side becomes concave, and thus a bending results. Since tropisms are brought about by differences in growth rate, they are usually rather slow, requiring from one hour to several days or longer for their completion. A common feature of tropisms is the fact that they result usually in placing the bending organ in a more favorable position with reference to the stimulus which induced the response. For example, light induces a **phototropism** (usually positive) of leaves and stems (Figures 122, 123, 124); this bending toward light is distinctly advantageous to plants, for leaves require light for photosynthesis. A root placed on its side exhibits a positive **geotropism** (Figure 125) (bending in re-

sponse to the earth's gravita-
tional force); this is beneficial,
for it results in the movement
of roots toward the soil, their
normal growth medium.
Stems usually exhibit negative
geotropisms, that is, they bend
upward from a horizontal po-
sition (Figures 126, 127). Roots
in rather dry soil grow toward
sources of moisture (Figure
129) (positive **hydrotropism**),
a reaction of advantage to
plants, for it enables roots to
secure further supplies of
water. Other tropisms in
plants are **chemotropism** (Fig-
ure 128) (growth reaction to
chemical agents) and **thigmo-
tropism** (growth reaction to
contact stimuli). These tro-
pisms constitute apparently
the chief means in most plants
of advantageous adjustment
to environmental influences.
In studying tropisms, students
should take care that they do
not attribute foresight or pur-
poseful reaction to plants. One
should not say that plants
bend toward the light *in order*

Fig. 123. Successive stages in the positive
phototropic bending of a bean seedling. Ex-
posures were made on the same plate at inter-
vals of 40 minutes.

to secure light, which they need, or that roots grow downward *in order*
to reach the soil. A more nearly scientific interpretation is this: that
stems grow toward light because light is a stimulus which affects their
growth in such a way as to cause them to bend toward it, and that
roots grow downward because gravitational force influences their
growth in such a manner that they bend downward.

Less common in plants are **turgor** movements, which are brought
about, not by differences in the rate of growth in different parts of
an organ, but by changes in the water content of certain cells in the

Fig. 124. Leaf-mosaic of buckeye (*Aesculus parviflora*).
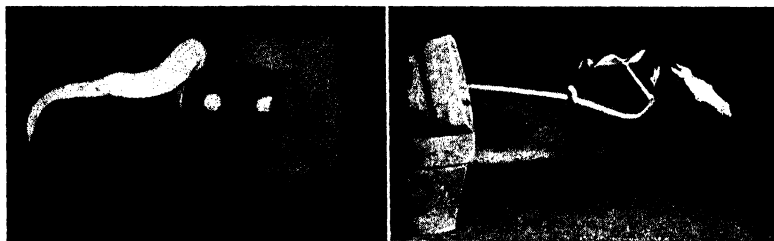
Fig. 125. Positive geotropism in primary   Fig. 126. Negative geotropism in young
root of bean.   stem of bean plant.

Fig. 127. Photographs of negative geotropism of bean stem; successive photographs made on same plate at intervals of 45 minutes.

reacting organs. Many turgor movements occur only in certain families of plants, particularly the legume family. They are usually more rapid than tropisms, requiring from a fraction of a second to 30 or 40 minutes for their completion. In some cases turgor reactions are beneficial to the organs in which they occur; in many instances, however, they are apparently devoid of significance. Common among turgor reactions are the **sleep movements** of the leaves of many plants, such as beans, peas, clovers, sheep sorrel (Figure 130), etc. The leaflets or leaves of such plants are normally in horizontal positions during the day, but fold together, often within a few minutes, when the light intensity decreases in late afternoon, or when light intensity comes exceedingly high, as during midday in summer. These sleep movements appear to be largely valueless to the plants in which they occur. The closing movements of the leaf-halves of the Venus'-flytrap are turgor movements; in this case, the reaction is one of obvious advantage to this species. The rapid movement of certain flower parts, such as the stamen reactions of barberry flowers and the stigma responses of *Torenia* flowers, are turgor movements which are beneficial in promoting the efficiency of insect pollination. In barberry flowers, the stamens (pollen-producing organs) grow upward and outward at an angle with the pistil of about 65°, just inside the petals; the inner, basal portion of each stamen is sensitive to contact and when it is touched, the stamen quickly snaps inward toward the center of the flower, dusting the insect visitors
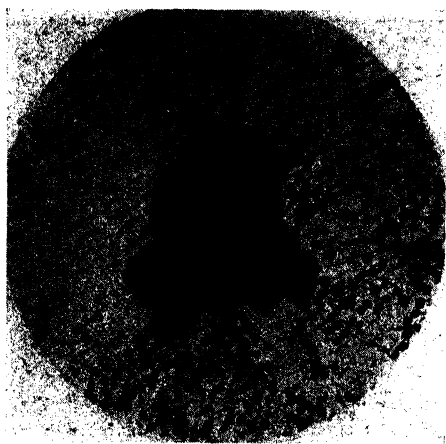
Fig. 128. Chemotropism in pollen tubes, which are shown growing toward a crushed stigma.

which normally provide the contact stimulus, with pollen, thus making more effective the insect-transmission of pollen. In the flowers of *Torenia*, catalpa, and trumpet-creeper, the two-lobed stigmas (the tips of the pistils, the innermost floral parts) are sensitive to contact and fold together quickly when they are touched (Figure 131). If the stigmas are not covered with pollen during their stimulation, they open after a several minutes closure; if however, as normally occurs, the stigma lobes are covered with pollen, either artificially or by an insect visitor, they normally remain closed, securing the pollen grains firmly between them. The movements of guard cells are further examples of turgor movements which are obviously of great importance to plants, since they control stomatal opening and closing. Doubtless most spectacular of all turgor movements is the rapid infolding of the leaflets and the sudden drooping of the whole leaves of the sensitive plant, *Mimosa pudica*. This leaf reaction, which is initiated by various stimuli, such as sudden contact and rapid temperature change, under optimum temperature and moisture conditions is completed within a few seconds. After one leaf drops and folds its leaflets, other leaves above and below the stimulated leaf react successively in similar fashion as the chemically transmitted excitation reaches them. After a period of some minutes, the leaves return to their original positions. It appears that these spectacular reactions of *Mimosa* leaves possess little if any biological significance.

In the turgor movements of guard cells, barberry stamens, *Torenia* stigmas, Venus'-flytrap leaves, and in certain other turgor movements, the plants in which these reactions occur obviously receive some benefits as a result of their ability to respond as they do to environmental stimuli. It should be emphasized again here that these plants do not purposefully react as they do in order to receive these benefits, but that the advantageous nature of these reactions is a result of the complex of physiological and morphological qualities which determine the

Fig. 129. As a result of their hydrotropic reactions, these roots have entered cracks in these drain pipes and have stopped up the pipes.

Fig. 130. Sleep movements in *Oxalis stricta*

Left. Day position of leaflets. Right. Night position of leaflets.
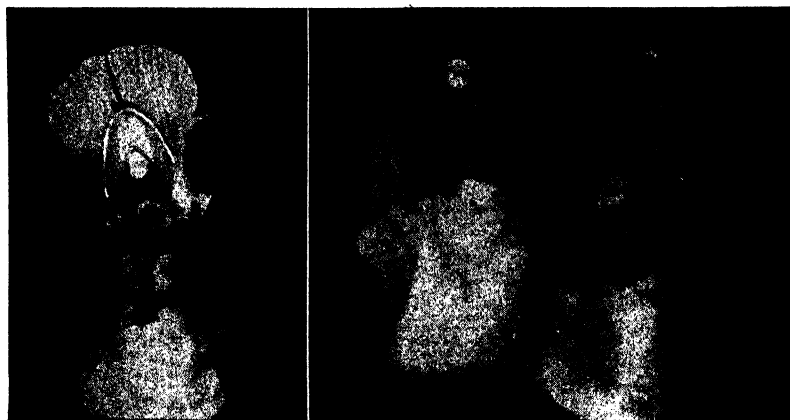
Fig. 131. Left. Flower of *Torenia*, showing 2-lobed stigma in center of corolla tube. Right. Unstimulated and stimulated stigmas of *Torenia* (corollas removed).

nature of the reactions induced by particular environmental stimuli. The Venus'-flytrap leaves, for example, do not react as they do *in order* to catch insects, but are able to entrap insects because they react as they do to the contact stimulation of their sensory hairs.

Taxic movements are movements of whole organisms or parts of organisms from one place to another. Since most plants are firmly anchored in the soil by their roots, taxic movements are rather infrequent in plants. They occur in certain unicellular aquatic motile algae and bacteria, and in swimming sperms and other types of reproductive cells in certain groups of plants. Taxic movements are caused chiefly by the rhythmic undulations of protoplasmic appendages (**cilia**, or **flagella**) which protrude into the water from the surfaces of these unicellular organisms. The direction of movement of such organisms is influenced by many external forces, particularly light, temperature, and chemical agents present in water.

8. SIMILARITIES BETWEEN PLANT AND ANIMAL REACTIONS

Some of the similarities between plant and animal reactions have already been mentioned — namely, the fact that generally the same kinds of stimuli induce responses in both groups of living organisms and that there is usually a transmission of excitation between sensory and reaction zones. In addition to these, there are other similarities

7. Plants react to many kinds of stimuli — light, gravity, chemical agents, etc. — by changing the positions of their organs.

8. The reception of stimuli by most plants is rather diffuse. Transmission of excitation in plants is principally by changes in the movement of plant hormones in growing tissues.

9. Movements of plant organs are chiefly the result of differences in the rate of growth of different tissues in an organ. The growth movements of cylindrical plant organs toward or away from stimuli are called tropisms.

10. A positive movement or reaction is one in the direction of origin of the stimulus. A negative reaction is one away from the point of origin of the stimulus.

11. Tropisms are classified on the basis of the stimuli which induce them — e.g., chemotropism, phototropism, etc.

12. Some plant movements are brought about by changes in the turgor pressure within certain cells of a stimulated organ. Among the turgor movements of plants are guard cell movements, "sleep" movements of leaves, stamen and stigma movements, movements in the leaves of Venus'-flytrap and sundew, and the movements of *Mimosa* ("sensitive plant") leaves.

13. Turgor movements are less common than tropisms, are executed more quickly, and in many cases seem to have no active importance in the lives of the plants in which they occur.

14. Tropisms constitute the principal means by means of which individual plants adjust themselves to their environments. Care should be taken not to assume the presence of foresight or reasoning intelligence in plants with respect to their advantageous adjustments to their environments.

15. There are many similarities between the responses of plants and those of animals.

The Structure and Functions of Flowers

1. REPRODUCTION IN FLOWERING PLANTS

THE ACTIVITIES thus far considered in flowering plants are termed **vegetative activities.** They involve the absorption of raw materials from the atmosphere and the soil, the synthesis of foods and other complex organic substances from these raw materials, the processes involved in growth, and the release and utilization of the potential energy of foods.

The **reproductive activities** of flowering plants, on the contrary, do not involve directly the absorption of raw materials and the elaboration of organic compounds therefrom, but result in the propagation of the species through the formation of offspring. Ordinarily vegetative activities begin in sprouting seeds and continue for a varying period of time before reproduction commences. As indicated in the preceding chapter, there is a very close relationship between vegetative and reproductive processes; the latter use enormous quantities of food, and usually begin only after considerable stores of food have accumulated in plant tissues following vegetative processes of varying duration.

The factors responsible for the beginning of reproductive activity following a predominantly vegetative phase are only incompletely known. Certain of these factors are internal in origin; the hereditary qualities of each species determine in part when reproduction begins; similarly, the nature and quantity of reserve foods exert an important influence upon the inception of reproductive processes. Recent investigations indicate that a flower-producing hormone (**florigen**) is an important agent in initiating reproduction in certain species of plants; whether this hormone is of common occurrence in plants and whether it is of major or minor importance in controlling the production of flowers are questions which will be answered by further botanical investigation. Among the important external factors which influence the onset of reproductive phases in the lives of various plants are the

daily duration of exposure to light, the carbohydrate-nitrogen ratio, and in many plants, temperature fluctuations. There are doubtless many other factors, both internal and external, and as yet undiscovered, which affect the reproduction of flowering plants.

In the angiosperms, the characteristic reproductive structures are **flowers.** A flower is interpreted by most botanists as a specialized reproductive twig, bearing specialized organs directly or indirectly involved in reproductive rather than vegetative activity. This chapter treats of the development, structure, and activities of flowers.

As described in previous chapters, reproduction in flowering plants is frequently brought about by the direct production of new plants from roots and stems, and less frequently, leaves. The formation of new individuals by bulbs, corms, rhizomes, tubers, runners, root "suckers," etc., is a common method of **vegetative reproduction** in many species of plants. The artificial propagation of plants by means of cuttings and grafts is likewise a method of vegetative reproduction.

2. THE ORIGIN AND STRUCTURE OF FLOWERS

Flowers develop from buds, as do other kinds of twigs. Some buds produce only flowers (elm, morning-glory, poplar), others produce both flowers and leaves (buckeye and apple), and cause increase in the lengths of stems in addition. Flowers differ from vegetative twigs in that there is virtually no elongation of their internodes, as a result of which floral organs are bunched together and not distributed at intervals along the stem, as are the vegetative leaves of most plants. Flowers also differ from vegetative twigs in that buds normally do not develop in the axils of floral organs as they do in the axils of green leaves of vegetative twigs. The parts of a flower develop as lateral protuberances of a bud growing point, just as do foliage leaves. The lowermost floral organs usually develop first, followed in order by the more apically situated parts, those nearest the tip of the bud enlarging last. The tip of a floral twig, from which the floral organs grow, is called the **receptacle.**

The commonest types of flowers, such as those of snapdragons, morning-glories, roses, irises, and petunias, are **complete** flowers; that is, they bear on their receptacles four kinds of floral organs: **sepals, petals, stamens,** and **carpels** (Figure 132). The outermost (lowermost) of these are the sepals, which, in most kinds of flowers, are small, green, leaf-like structures. The sepals enclose and protect the other floral
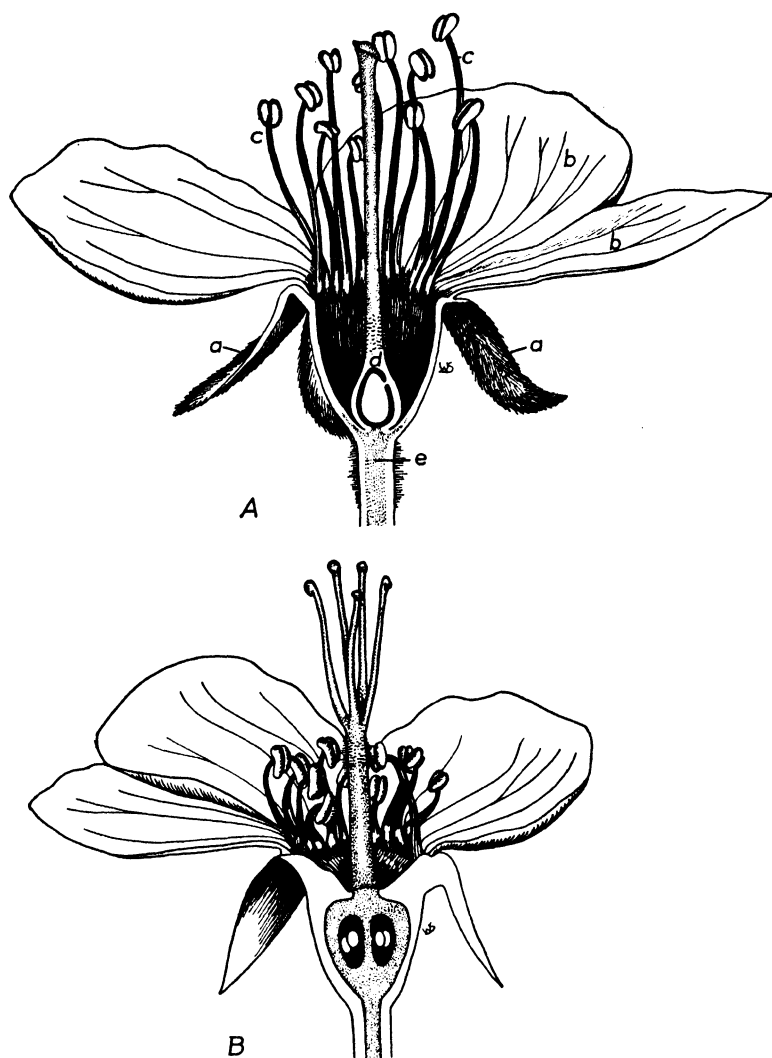
Fig. 132. Longitudinal sections of flowers

A. With superior ovary (plum): a. sepals, b. petals, c. stamens,
d. pistil (composed of carpels), e. receptacle.
B. With inferior ovary (apple).

organs in the bud before they are fully developed. The sepals collectively are called the **calyx.** Above (inside) the sepals are the usually showy, conspicuous, often brightly colored **petals,** known collectively as the **corolla.** The number of petals in a flower is usually the same as that of the sepals, or sometimes a multiple of the sepal number. In buttercups, for example, there are 5 sepals and 5 petals. Single roses have 5 sepals and 5 petals; in double roses with many petals, the number of petals is usually a multiple of 5. Petals serve primarily to attract insects, the visits of which to flowers are important in the reproductive functions of flowers. Petals secure the attention of insects in several ways. The bright colors of many flowers are attractive to insects. The petals of some flowers have glands (**nectaries**) which secrete **nectar,** a sweetish liquid which is much desired by bees and other kinds of flower-visiting insects. The odors of the essential (aromatic) oils and other substances produced by the petals of many species of plants constitute another means of luring insects to flowers. In many species, floral fragrances are very pleasant to the human sense of smell; the characteristic odors of jasmine, rose, lavender, sweet pea, carnations, and others arise from the oils secreted by petals. Many of these oils are important in perfume manufacture. In a few species, such as skunk-cabbage, some hawthorns and Dutchman's pipe (*Aristolochia*), the floral odors are very strong and exceedingly unpleasant, sometimes in such degree that they cause nausea in human beings. These offensive odors attract chiefly the kinds of insects which commonly visit decaying animal flesh and other rotting, ill-smelling organic matter. Many flowers of this type are colored maroon or reddish-brown and frequently resemble animal flesh. The insects, such as bees, which visit pleasantly scented flowers are not attracted by flowers of the latter type.

Inside (above) the petals are the **stamens,** which produce pollen grains. A stamen consists usually of a slender stalk, or **filament,** which bears at its apex a single, enlarged, often more or less cylindrical or ovoid **anther.** Within anthers develop the pollen grains which later lead to the formation of male reproductive cells, or **sperms.** In the center of a complete flower is situated a **pistil,** which consists usually of three fairly distinct portions — an enlarged, globose **ovary,** within which the seeds are formed, an elongated, slender **style,** which rises from the top of the ovary, and at the top of the style, a slightly enlarged **stigma,** upon which pollen grains fall or are brought, previous to the fertilization of the immature seeds, or **ovules.** Stigmas are frequently very rough or bristly, and sometimes they are covered with a sticky fluid, as

a result of which pollen grains are more securely held on the stigmatic surfaces. A pistil is composed of one or several **carpels,** or seed-bearing organs. If a pistil is made up of one carpel, as it is in the flowers of peas, beans, and buttercups, it is called a **simple pistil.** In the flowers of tulips, snapdragons, lilies, and many other species, 2 or 3 or more carpels are fused together into a single **compound pistil** (Figure 133). The flowers of buttercups, anemones, clematis, and strawberry bear numerous simple pistils; in peas and beans, each flower has but one simple pistil.

Sepals and petals are frequently termed the **accessory parts** of flowers because they are not directly concerned with reproduction processes. Stamens and pistils are the **essential parts** of flowers for they are involved directly in the production of seeds. The accessory parts are frequently of indirect importance in reproduction in that they may attract insects, which are necessary for the pollination of many types of flowers.

Fig. 133. Types of pistils
A. Simple pistils (*Sedum*).
B. Compound pistil with 2 free styles (carnation).
C. Compound pistil with 1 style (snapdragon).
r. receptacle.

The four kinds of floral organs described above — sepals, petals, stamens, and carpel(s) — are present in all complete flowers. Not all flowers are complete, however; in some plants, such as anemone and clematis, there are sepals, stamens and pistils present, but no petals. In oat flowers, stamens and pistils are present, but sepals and petals are lacking (Figure 137). In willows, there are two kinds of flowers, some which bear stamens, others which bear pistils; in both types, neither sepals nor petals are present. All flowers, such as those of willow, oats, clematis, and anemones, which lack one or more of the four kinds of floral organs, are called **incomplete.** Species, such as

Fig. 134. Staminate (left) and pistillate (right) inflorescences of cottonwood, *Populus deltoides*. Cottonwoods are wind-pollinated.

willow, oak, walnut, and cottonwood (Figure 134), in which the stamens and pistils are produced in separate flowers, are said to have **imperfect flowers.** Imperfect flowers which bear stamens are termed **staminate,** those which contain pistils are called **pistillate.** In willows, cottonwoods, hemp, and many other species, staminate flowers and pistillate flowers are borne on separate plants, a condition described as **dioecious.** The staminate and pistillate flowers of other species, such as walnuts, oaks, and corn (Figures 135, 136), are produced by the same plant; such plants are **monoecious.** Tulips, lilies, roses, sweet peas, and orchids have flowers in which stamens and pistils are present in the same flower; such flowers are termed **perfect.** A flower may be perfect but incomplete; for example, oat flowers are perfect because they bear both stamens and pistils, and they are incomplete, because they lack sepals and petals. All imperfect flowers are obviously incomplete.

There are many other kinds of variations in the structure of flowers of different species of angiosperms. The numbers of parts, the sizes and colors of petals, the relative positions of the various floral organs, the degree of fusion among parts, are chief among the varying characteristics of the flowers of different species of plants.

Fig. 135. The staminate flowers of corn.
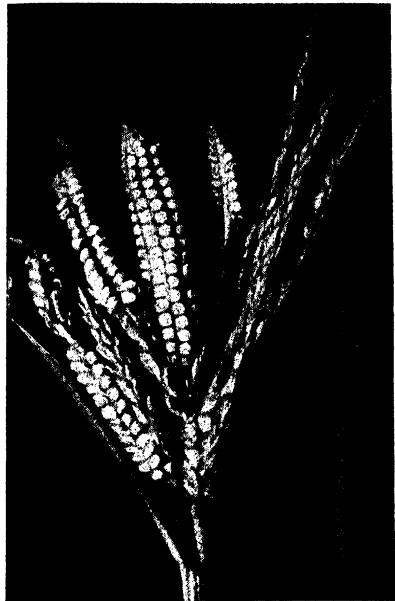
Fig. 136. An abnormal corn tassel, bearing ears of pistillate flowers, and also staminate flowers.

A

B
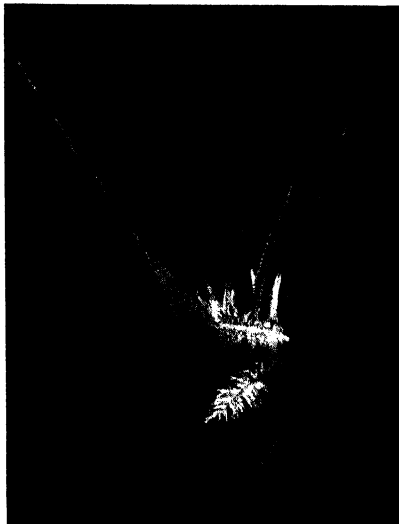
Fig. 137. A. An oat spikelet, showing two flowers ready for pollination. B. A fully developed oat flower, showing styles (a), a filament (b), and anthers (c).
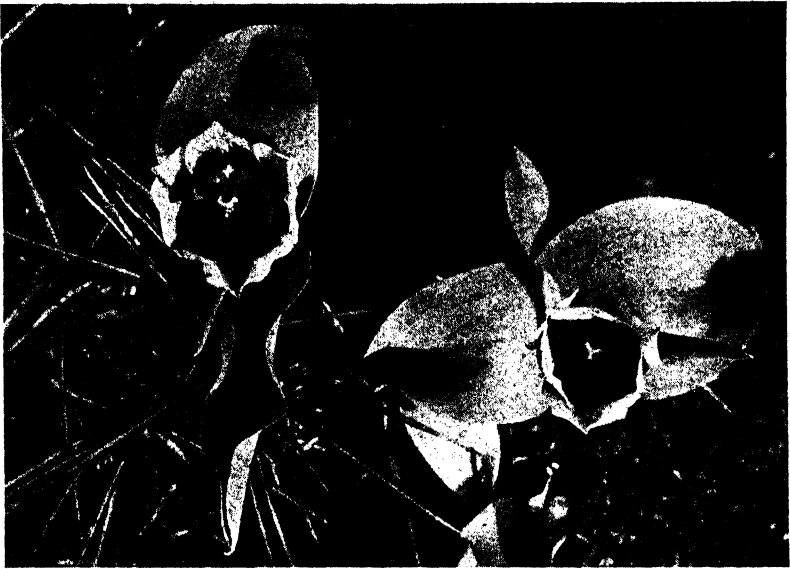
Fig. 138. Tulips are monocotyledons. Note the 3 sepals, 3 petals, 6 stamens, and compound pistil with a 3-branched stigma.

A   *B*
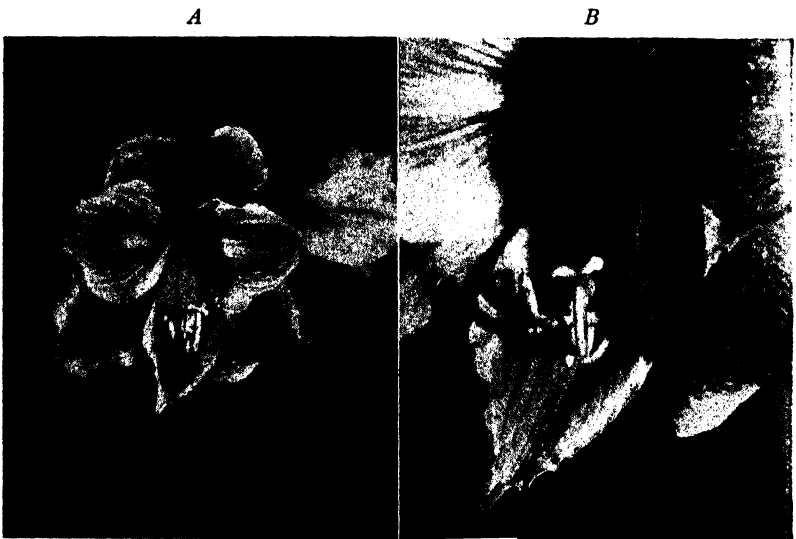
Fig. 139. A. Flower of amaryllis, a monocotyledon, showing 3 sepals, 3 petals, 3-branched stigma, and 6 stamens. B. Close-up of stamens and stigma of amaryllis flower.

Fig. 140. Flowers of *Aquilegia* (columbine), a dicotyledon with flower parts in 5's. Notice spurred petals, sepals, and numerous stamens.
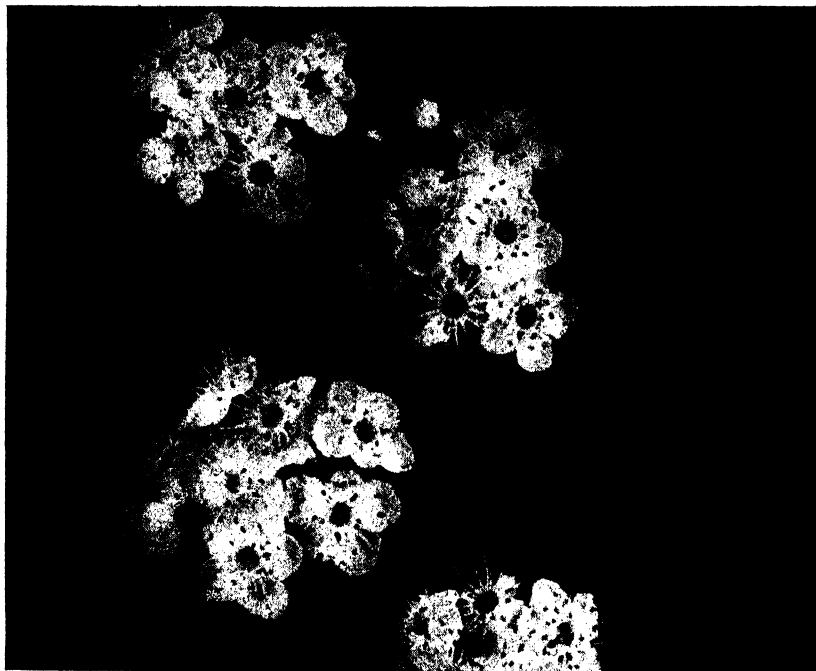
Fig. 141. Flowers of hawthorn, a dicotyledon, member of the rose family.

The flowers of monocotyledons (about 40,000 species) generally have their flower parts in 3's or multiples of 3. In tulip flowers, for example, there are 3 sepals, 3 petals, 6 stamens, and a pistil of 3 fused carpels (Figure 138). In iris flowers, the same numbers of parts are found, except that there are only 3 stamens. The same basic numbers of parts are found in most other monocot families — grasses, amaryllises (Figure 139), bananas, pineapples, palms, and orchids. In dicotyledons (about 155,000 species) flower parts are chiefly in 4's or 5's (Figures 140, 141, 142), less frequently in 2's, and in only a few families in 3's. In the flowers of *Sedum* and certain other members of the live-forever family, there are 5 sepals, 5 petals, 10 stamens, and 5 separate, simple pistils. The flowers of evening-primroses have 4 sepals, 4 petals, 8 stamens and a compound ovary of 4 fused carpels. In members of the bleeding-heart family, the flowers have usually 2 sepals, 4 petals, 6 stamens, and a compound pistil of 2 fused carpels. Magnolias and paw-paws are among the relatively few dicotyledons in which the sepals and petals are in multiples of 3.

Photo by Missouri Botanical Garden

Fig. 142. The flowers of peonies are considered primitive. Notice the numerous stamens and the separate, simple pistils in the center of each flower.

Petals vary greatly in their size, color, and arrangement in flowers. In buttercups, petunias, and roses, the petals are equal in size and are equally spaced in position, so that the flowers of which they are parts are built on a circular plan, as viewed from above. This type of symmetry is termed **radial symmetry** (Figures 143, 144). In other species of flowering plants, such as sweet-peas, snapdragons, orchids, and mints, the petals vary in size and are unequally spaced, so that flowers of this type are constructed upon a right-and-left plan rather than a circular plan. This right-and-left plan of floral construction is called **bilateral symmetry** (Figures 145, 146, 147).

In many flowers, such as roses and magnolias, the floral organs are all separate and distinct from each other. The flowers of petunias, phlox, and sunflowers on the contrary show a considerable degree of fusion among their floral organs. In petunia and phlox flowers, the petals are fused into trumpet-shaped and tubular corollas respectively. In sunflowers, the petals are fused and the stamens are likewise fused by
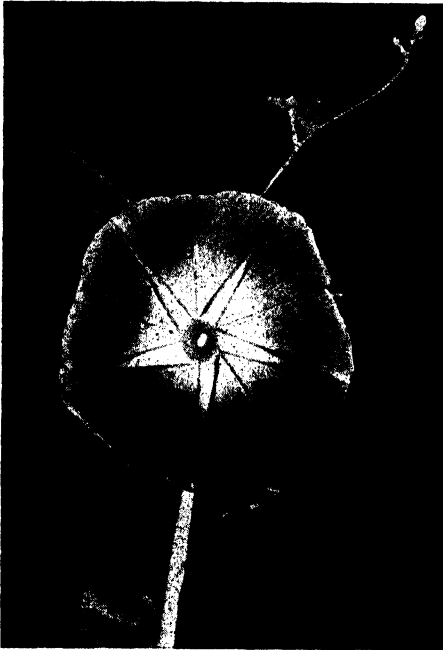
Fig. 143. A morning-glory (*Ipomoea*) flower has a trumpet-shaped, radial corolla of 5 fused petals.

their anthers into a tube around the style. The degree of fusion of various flower parts thus differs widely among different species of flowering plants.

In some kinds of flowers, such as magnolia and water lilies, the floral organs are arranged in **spiral** fashion on the receptacle — that is, all the floral organs from lowermost to uppermost can be connected by a continuous, spiral line or several spiral lines. In lilies, phlox and many other species, the flower parts are arranged in distinct circles or cycles upon the receptacle and cannot be connected by a spiral line. This **cyclic** arrangement of parts is more common than the spiral arrangement and is considered a more advanced condition.

Flowers also vary in the positions of their ovaries with respect to the places of attachment of sepals and petals on their receptacles. In snapdragons and morning-glories, the sepals and petals are attached to the receptacle just *beneath* the point of attachment of the ovary to the receptacle. In evening-primroses, and honeysuckles in contrast, sepals, petals and stamens grow out from the *top* of the ovary, which is sunken in the receptacle. Ovaries of the first kind — those situated above the points of origin of sepals and petals — are termed **superior.** Those ovaries of the second type, with the sepals and petals arising at their crests, are called **inferior** (Figure 132).

Flowers vary also in their relative positions on the plants which produce them. In magnolias, most roses, and tulip trees, each flower is solitary, borne on a single stalk at some distance from other flowers. In snapdragons, lilacs and asters, several or many flowers are borne in clusters. These flower clusters, or **inflorescences** (Figure 148), differ markedly in the number of flowers which they bear, the number and
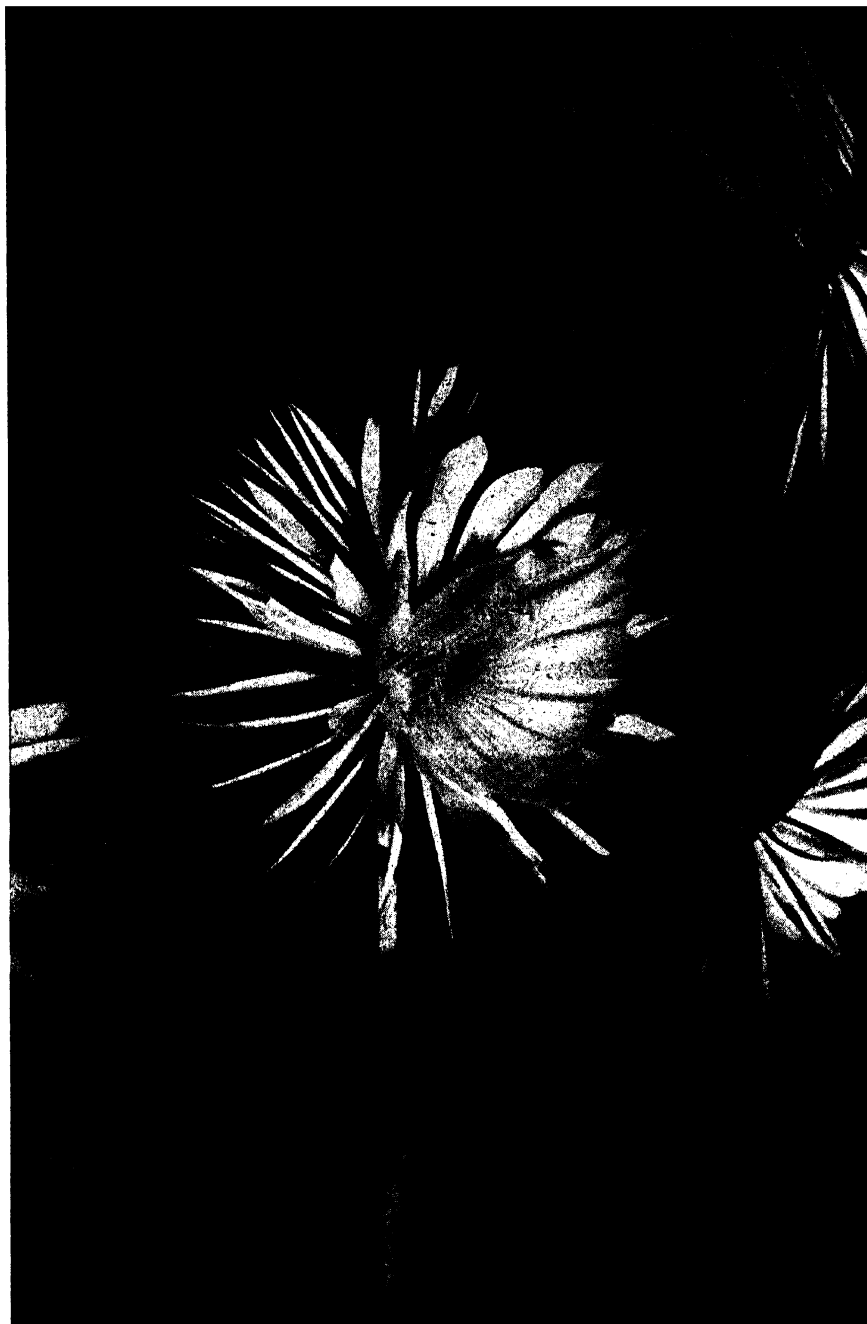
Fig. 144. Flowers of night-blooming cereus, a dicotyledon of the cactus family.

Photo by Missouri Botanical Garden

Fig. 145. The flowers of this orchid (*Cattleya* hybrids) are bilaterally symmetrical.

arrangement of their branches, etc. One of the most highly developed types of flower clusters is that found in members of the **composite** family (sunflowers, asters, zinnias, daisies, etc.). The characteristic inflorescence of composites is called a **head** (Figure 149). In a head, the flowers are usually very small and are tightly crowded on a flattened or convex, disc-shaped, compound receptacle. The corollas of the marginal flowers on these discs are frequently much enlarged and brightly colored. These **rays,** as they are technically called, are commonly and erroneously called petals. Each of the so-called "petals" of a sunflower head, for example, is really the yellow corolla of a ray flower. The flowers which occupy the central part of the sunflower head have much smaller, less conspicuous corollas than do the ray flowers; further, the disc flowers are radially symmetrical whereas the ray flowers are bilaterally symmetrical. In sunflowers, as in many other composites, the disc flowers produce seeds, whereas the ray flowers are sterile. The whole "sunflower" is thus not a single flower, but a flower-cluster with many dozens of tiny flowers. In many kinds of inflorescences, special, modified leaves called **bracts** frequently grow out from the main stalk (**peduncle**) of the inflorescence (Figure 150). Each bract is usually situated at the juncture of the individual flower stalk (**pedicel**) with the peduncle in such fashion that the flower is in the axil of its bract, just as a vegetative twig is in the axil of a leaf. These bracts are sometimes small, as in snapdragons, or sometimes larger and brightly colored, as in poinsettias. Bracts sometimes attract insects or offer protection to the flowers in their axils, but in many cases they seem devoid of function.

Flowers vary in many other ways. They differ in their periods of

blooming, the nature of their insect visitors, their methods of pollination, their length of life, the abundance of their pollen, the numbers and locations of the ovules in their ovaries, etc.

These many diverse features of flower structure furnish the chief criteria used to distinguish among various species of flowering plants and to classify such plants into related groups. On the basis of their studies of fossil plants, of the anatomy of the flowers of present day plants, of the developmental histories of flower parts, etc., botanists have demonstrated that evolution has occurred among the angiosperms and that certain types of floral structure are to be regarded as ancient and primitive, others as more recent and more advanced. Among the earliest known fossils of true flowering plants are those of magnolias, tulip trees, and related species, the solitary flowers of which have usually rather numerous stamens and pistils, a spiral arrangement at least of stamens and pistils, a complete lack of fusion among the various floral organs, radially symmetrical corollas, superior

Photo by Missouri Botanical Garden

Fig. 146. The bilaterally symmetrical flowers of the dove orchid, a monocotyledon. The head of the "dove" is the column, which is a structure composed of a pistil, bearing a functional stamen near its apex.

ovaries, and frequently a considerable variability in the numbers of stamens and pistils in different flowers of the same species. Since these characters are found in what were apparently the first true angiosperms, they are assumed to be primitive. In those species of angiosperms which have appeared more recently in the earth's history and which are unknown as fossils, floral characters are often very different from those of more ancient flowering plants. The major differences among primitive and more advanced angiosperms with respect to floral structure are presented in the following table:

Photo by Missouri Botanical Garden

Fig. 147. An inflorescence of banana, showing the large terminal bud of the inflorescence, and the clusters of bilaterally symmetrical flowers with inferior ovaries which ripen into the edible bananas of commerce.

Primitive Characters	*Advanced Characters*
1. Large, variable numbers of parts	1. Smaller, constant numbers of parts
2. Spiral arrangement of parts	2. Cyclic arrangement of parts
3. Solitary flowers	3. Flowers borne in clusters
4. Parts separate	4. Parts fused
5. Superior ovaries	5. Half-inferior and inferior ovaries
6. Radial symmetry	6. Bilateral symmetry

Among plants which are considered to have rather primitive or intermediate types of flowers are magnolias, buttercups, barberries, tulip trees, anemones, roses, and geraniums. Species which have more advanced types of flowers are mints, petunias, snapdragons, honeysuckles, morning-glories, Canterbury bells, and composites. Relatively few species of angiosperms have flowers with exclusively primitive or advanced characters. More commonly flowers possess varying combinations of advanced and primitive structural features.

A   B
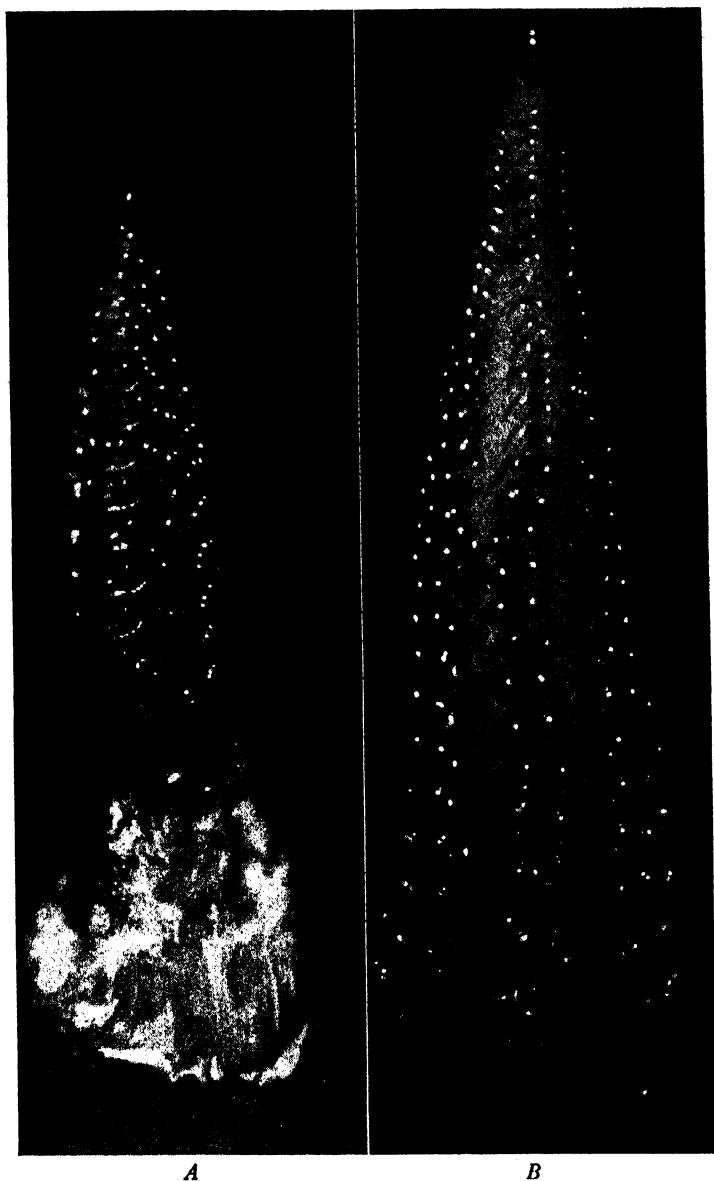
Fig. 148. Early stages in the development of barley (A) and corn (B) inflorescences. Notice the smooth, convex, apical growing points, with the spikelets developing as lateral outgrowths from them.
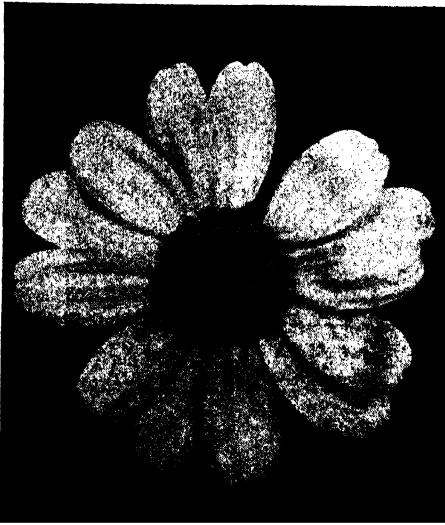
Fig. 149. A composite inflorescence of *Cineraria*. Notice the large bilateral corollas of the ray (marginal) flowers and the smaller, radially symmetrical disc flowers. Note the 2-branched styles of the disc flowers.

Photo by Missouri Botanical Garden

Fig. 150. Inflorescences of dogwood (*Cornus florida*). Each inflorescence consists of several very small flowers subtended by 4 large, white bracts.

Photo by C. F. Hottes
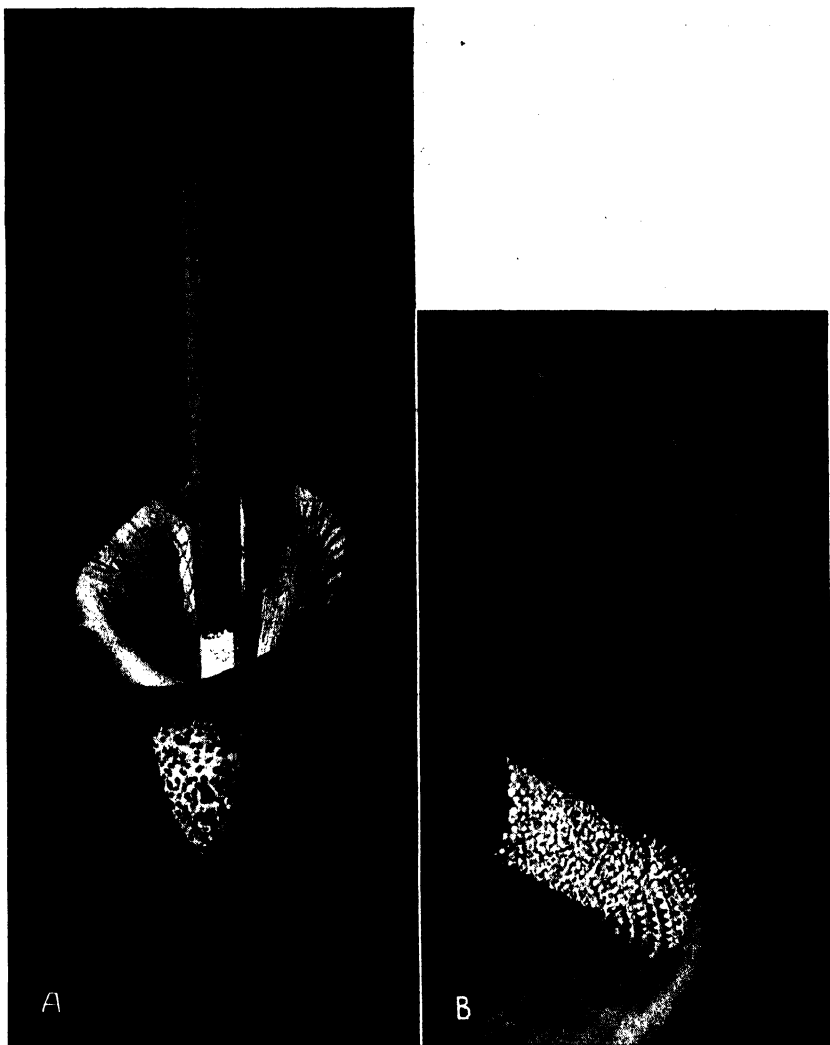
Fig. 151. A. Inflorescence of *Amorphophallus titanum*, a tropical member of the aroid family. The tiny flowers are crowded on the basal portion of a cylindrical, fleshy spike, the spadix, which is surrounded by a large, flaring bract, the spathe.

B. An enlarged portion of the base of the spadix of *Amorphophallus*. The flowers at the base of the spadix are pistillate, the smaller flowers just above them are staminate. The upper part of the spadix bears no flowers.

3. THE POLLINATION OF FLOWERS

Pollination is the first of a series of processes which result in the formation of seeds, and as such is exceedingly important in the lives of seed plants. Pollination in angiosperms may be defined as the transfer of pollen grains from an anther to a stigma. The transfer of pollen from the anther of a flower to the stigma of a flower of another plant is called **cross-pollination,** as contrasted with **self-pollination,** in which pollen is carried from an anther to the stigma of the same flower or to another flower of the same plant. In some species (e.g., orchids) only cross-pollination occurs, in others (e.g., peas) self-pollination is the rule. Cross-pollination is effected both by wind and insects and occasionally by water.

Although cross-pollination is the more common phenomenon, nevertheless self-pollination occurs in the perfect flowers of many species of flowering plants. Among such species are wheat, peas, oats, barley, tobacco, and cotton which are normally chiefly self-pollinated. In tobacco, peas, and other flowers, the stigma is usually covered by the flower's own pollen before the corolla opens. Bees visiting such flowers may bring about a certain amount of cross-pollination, but the flowers of tobacco, peas and cotton, for example, are able to produce large quantities of seeds as a result of self-pollination exclusively. Flowers which produce seeds following self-pollination are termed **self-fertile,** while those which form seeds only as a result of cross-pollination are said to be **self-sterile.** In certain varieties of pears, grapes, and other plants, the flowers are chiefly cross-pollinated. In the failure of cross-pollination, the self-pollination of such flowers often occurs, with the result that some fruits and seeds are formed, although they are usually fewer and smaller than fruits and seeds produced by cross-pollination. Horticulturists advise the establishment of beehives in orchards to insure cross-pollination of the flowers of fruit trees so that the fruit crop may be large and of superior quality.

The natural agents of pollination in flowers are most commonly wind and insects, less frequently birds and water. Bees and various types of moths are the most common insect visitors of flowers (Figures 158, 159). Various kinds of birds, particularly humming-birds in search of nectar, are important in the pollination of certain kinds of flowers. In most species of flowering plants, insects are the most common agents of pollination. Insect-pollinated and wind-pollinated flowers exhibit fundamental structural differences which reflect their different modes

THE POLLINATION OF FLOWERS

Photo by Missouri Botanical Garden   *Photo by C. F. Hottes*

Fig. 152. Walnut twig, showing staminate flowers in pendulous spikes (catkins) with 2 pistillate flowers near apex of twig. Each pistillate flower has a large ovoid ovary with 2 style branches. Walnut flowers are all wind-pollinated.

Fig. 153. The staminate flowers of alder are borne in long, pendulous catkins. The pistillate flowers are in globose erect catkins. Alders are wind-pollinated.

of pollination. Wind-pollinated flowers, such as those of cottonwoods, walnuts, oaks, corn, wheat, and oats, usually lack petals, odor, and nectar, are usually borne in rather dense clusters, produce copious pollen, and have stigmas which are greatly enlarged, or which are equipped with long hairs or bristles which catch and hold pollen grains as they are blown through the air (Figures 152, 153, 154). Flowers, such as those of roses, orchids, apples, and sunflowers, which are pollinated by insects and birds generally possess rather large and conspicuous petals, secrete nectar or aromatic substances (or both), produce much smaller quantities of pollen than do wind-pollinated flowers, and usually have stigmas which are small or only moderately large and which lack the characteristic hairs and bristles of many wind-pollinated flowers (Figures 144, 145, 155). Many insect-pollinated flowers lack conspicuous corollas but have in their place brightly colored sepals (four-o'clock), showy stamens (willows, eucalyptus), or large bracts (dogwood, poinsettia). In the composites, the individual flowers, which are chiefly insect-pollinated, are tiny, but the heads in which they occur

Photo by O. T. Bonnett

Fig. 154. Tip of mature style ("silk") of corn, showing pollen grains.

are usually conspicuous, chiefly because of the large corollas of the marginal, ray flowers.

It is probable that the odors of flowers are more important than colors in attracting insects, for many insects seem to have rather imperfect vision and rather sensitive sense of smell. Flowers pollinated by bees and butterflies, which are active during the day, are usually more fragrant during the day than they are at night, whereas flowers pollinated by moths, which are nocturnal in their habits, are ordinarily more fragrant at night. Flowers pollinated by moths are open at night and are commonly white.

The nectar secreted by the nectaries of many kinds of flowers is greedily sought by bees, butterflies, moths, and other insects, which use the sweetish nectar as food. Nectar collected by bees is taken into the honey sac, an enlarged portion of the digestive tract, in which the nectar is mixed with saliva. This mixture is then poured out into hexagonal waxy compartments of a honeycomb and is evaporated to a syrupy consistency by the fanning of the worker bees. This syrupy material, consisting of water, sugars, chiefly glucose and levulose, and usually some aromatic substances, is honey. The flavor of honey is in large part a result of the aromatic substances carried away from flowers by bees. Thus, honey made from the sweet-scented flowers of some legumes (particularly the clovers), of linden, and of orange blossoms, is especially prized. Adult bees use nectar as food and carry pollen to their hives, where it serves as food for the larvae. So much pollen is ordinarily gathered, however, that not all is eaten, and thus there are always some pollen grains which are accidentally carried to other flowers visited by bees.

A cross-section of anther shows the presence of usually two **pollen-sacs**, within which the **pollen grains** are produced. When an anther

Fig. 155. Bees entering snapdragon flowers.
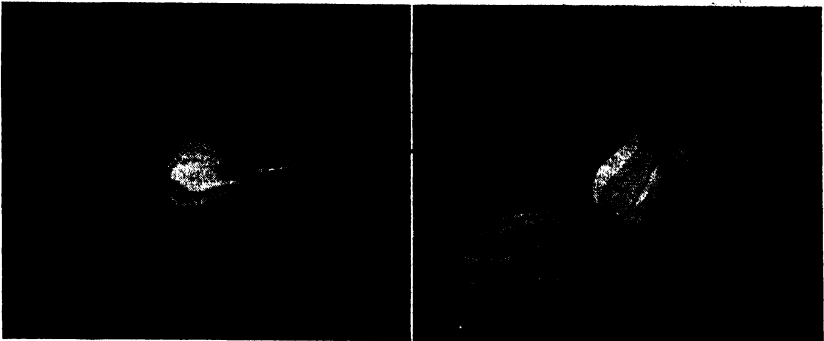
Fig. 156. Proterandry in a flower of *Clerodendron*. In the flower at the left, the stamens are mature; the style is immature and is still curled downward. In the flower at the right, the stamens have shed their pollen and have begun to dry up; and the style is now erect and capable of pollination.
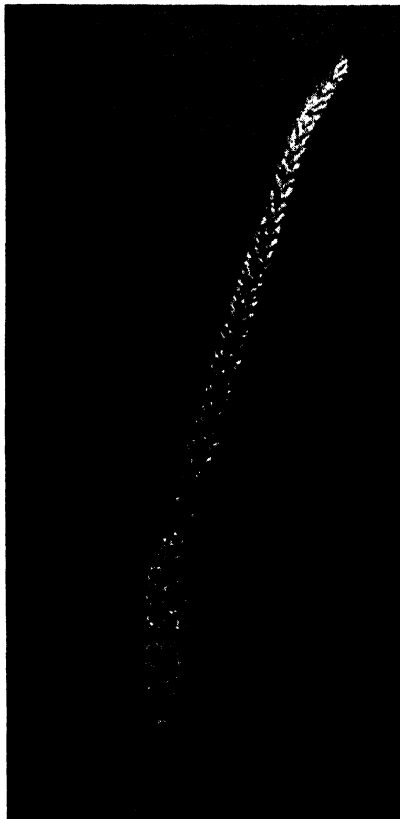
Fig. 157. Proterogyny in plantain (*Plantago major*) flowers. The young flowers (upper half of spike) have mature, white styles and immature stamens. In the older flowers (lower half of spike) the pistils have been pollinated, the styles have dried up, and the stamens are now mature and shedding pollen.

reaches maturity, the pollen-sacs open, usually by longitudinal splits and the pollen grains are thus exposed to the air and are ready for transfer to a stigma.

In many species of plants, it seems that greater vigor is shown by the offspring of cross-pollinated flowers than by those of self-pollinated flowers. This fact, together with the facts that the flowers of most species of flowering plants are cross-pollinated and that there exist in these flowers many modes of behavior and highly specialized devices to insure cross-pollination, indicates that this type of pollination seems to be a rather highly advanced type.

Among the ingenious methods which ensure cross-pollination or make it more effective are the following:

1. **Imperfect flowers.** Self-pollination in these flowers is obviously impossible, for stamens and pistils are borne in separate flowers, often on separate plants (Figures 134, 135, 136).

2. **Chemical incompatibility between pollen and stigma.** In rye, pollen grains cannot germinate on stigmas of the flowers of the same plant which produces the pollen, a condition known as **self-sterility.** In certain orchids, the stigmas of the flowers are poisonous to the pollen from flowers of the same plant, but not to pollen from flowers of other plants of the same species. In other species of orchids, pollen is poisonous to the flowers of the same plant, often causing them to shrivel. Placed on the stigma of the flowers of other plants, the pollen grains are capable of fertilizing the undeveloped seeds.

3. **Differences in time of maturation of stigmas and stamens.** In the flowers of some species of plants (e.g., sunflower, cornflower, salvia, verbena), the stamens of the flowers mature and shed their pollen before the stigmas of the same flowers are sufficiently mature to receive pollen. Thus, self-pollination of such flowers is impossible, for when the stigmas are ready for pollination, the only pollen available is that from other flowers. This maturating of the stamens before the stigmas of a flower are capable of receiving pollen is called **proterandry** (Figure 156). The opposite condition, known as **proterogyny** (Figure 157), in which the stigma of a flower is mature and ready for pollination before the stamens of the same flower mature, is much less common than proterandry. Proterogyny is conspicuous in plantains, magnolias, avocados, and many other species.

4. **Specialized structural mechanisms.** The flowers of many species of plants possess specialized structures or arrangements which promote the efficiency of cross-pollination, especially by insects. Among the most interesting and most effective of these specializations are:

a. *Heterostyly.* In some plants, such as sheep-sorrel, loosestrife, buckwheat, and Chinese primroses, the stigmas and stamens are inserted in the flowers at different levels. In some flowers of Chinese primroses, there are long styles, which lift the stigmas high in the flowers, and short stamens which are situated deep in the corolla. In other flowers of the same species, the stamens are borne high on the corolla and the styles are very short, so that the stigmas are situated low in these flowers. The stamens in the long-styled flowers are at about the same level as the stigmas of the short-styled flowers, and the stamens in the short-styled flowers are at the same height as the stigmas of the long-styled flowers. These relations between the stamens and stigmas of the two types of flowers have this result: that an insect which visits one type of flower collects pollen on its body in a place which will touch the stigma of the other type of flower when it visits the second flower. When pollen from the low stamens is placed upon low stigmas, or pollen from high stamens is placed upon high stigmas, a much higher yield of good seeds is obtained than that achieved through the self-pollination of these flowers.

b. *Spring devices of stamens.* In some flowers, such as those of *Salvia*, two pollen-producing stamens are set upon spring-like devices inside the corolla, near its mouth. When a bee visits a *Salvia* flower, it enters the mouth of the two-lipped corolla tube and presses against the spring device which causes the stamens to bend downward and dust the

Fig. 158. Bee pollinating a flower.

Fig. 159. Bee pollinating a composite head.
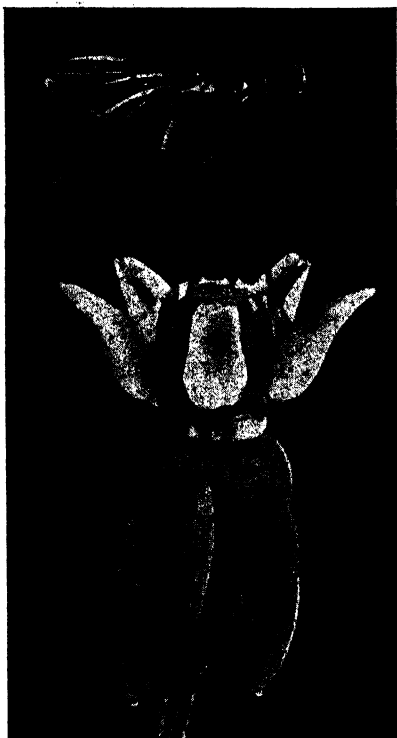
Fig. 161. An insect with milkweed
pollinia on its legs.

Fig. 160. Insect on milkweed flower.

bee's back with pollen. The pistil
matures several days later, after
the pollen has been shed; the style
curves out in such manner that
the stigma hangs about halfway
between the upper and lower lips. When a bee visits a *Salvia* flower in
this stage, the stigma strikes the back of the bee in approximately the
same place where pollen was deposited by the stamens of another *Salvia*
flower. Thus cross-pollination is effected.

c. *Pollination mechanism of milkweed flowers.* In milkweed flowers,
there are narrow, vertical slits between the anthers, which are fused
into a ring around the pistil. At the top of each of these slits is a tiny
structure, the translator, to the ends of which masses of waxy pollen
grains are attached. When an insect crawls over a milkweed flower,
one of its legs is likely to become caught in one of these slits (Figure 160).
The insect begins to struggle to free its trapped leg and, if it is strong
enough, it succeeds. Because of the rapid motion of the wings, the insect
rises and its entrapped leg slides up the slit, carrying away the translator
with its pollen masses as the leg is freed (Figure 161). When the insect

visits other milkweed flowers, it leaves on their stigmas the pollen masses which have become fastened to its legs during the earlier visits to other flowers. In milkweed flowers, many dead insects, caught by their legs, may be found.

d. *The pollination of Yucca flowers* (Figures 162, 163). In *Yucca* (Spanish bayonet) flowers, the styles are hollow, with a longitudinal canal, at the lower end of which the stigmatic surface is located, so that pollination is not possible unless pollen reaches the bottom of this tube. The only insect capable of pollinating *Yucca* flowers is the *Yucca*-moth (*Tegeticula alba*). The female moth by means of specialized mouth parts collects pollen from several stamens, then with her egg-laying device drills a hole through the wall of a *Yucca* ovary and lays her eggs among the ovules, or undeveloped seeds of the *Yucca* ovary. Fol-

Photo by Missouri Botanical Garden

Fig. 162. Plants of Spanish bayonet (*Yucca*), a monocotyledon.

lowing the deposition of her eggs, the moth carries the pollen, which she has gathered, to the top of the pistil and forces it down the canal to the stigmatic surface at the bottom. Thus pollination is accomplished. The larvae develop in the *Yucca* ovary among the growing ovules which were fertilized by the pollen deposited by the female moth in the bottom of the canal. The larvae eat some of the *Yucca* seeds, but usually leave enough seeds for the propagation of the *Yucca* plants. At maturity, the larvae bore out through the ovary and spin threads by which they lower themselves to the ground. They then form cocoons in the soil and in the following spring the mature moths emerge just before the *Yuccas* flower again. The striking features of the *Yucca* and *Yucca*-moth relation-

Fig. 163. Flowers of *Yucca glauca stricta*. Note the blunt hairy stamens (6 per flower) and the central pistil with an opening at its apex.

ship are these: that *Yucca* flowers can be pollinated in nature *only by Yucca* moths, that the larvae of the moths can derive nourishment from *Yucca* ovules and from *no other* kind of food, and that both *Yuccas* and *Yucca*-moths can complete their life cycles only with the aid of each other. This is one of the most amazing cases known of absolute interdependence of a plant and an animal for the completion of their life histories.

There are many other mechanisms and modes of behavior in flowers which promote cross-pollination or which otherwise influence pollination phenomena. For example, in many two-lipped flowers, such as snapdragons, the stamens are located under the upper lip in such position that they are not exposed to rain. Thus their pollen is not washed away by raindrops as it is in many other kinds of flowers. In many composites, the style branches at its apex into two outward-curved stigmas. Just below the stigmas are five anthers united into a ring above the style. Normally, composite flowers are cross-pollinated by insects, but if such pollination is not consummated, the stigmas resume their outward and downward curving until they touch the anthers from which they pick up pollen grains. In some flowers, such as those of

Schizanthus, or poor-man's-orchid, the stamens are so situated that they spring forward very abruptly when an insect touches the flower and scatter their pollen on its body. Among the most complex floral mechanisms and adaptations to insect pollination are those found in the thousands of species of the orchid family, in the flowers of which the fertile stamens and stigma are actually borne upon the same structure, called the column. Orchids are completely dependent upon insects for their pollination, in many species to the extent that an individual orchid species can be pollinated by only one kind of insect.

4. FERTILIZATION IN FLOWERS

After pollen grains (Figure 165) are deposited on a stigma by wind, insects, or some other agent, swellings appear in the thin places in their walls. The pollen grains absorb water and other materials from the stigma, and style, and use these substances, together with the foods stored within them, in the production of **pollen tubes** (Figure 164). Each pollen grain normally produces a single pollen tube. A pollen tube, which begins as a swelling as mentioned above, continues its growth downward through the style, either by digesting the cells of the style or by passage downward through a central canal present in the styles of some flowers. The lengths attained by some pollen tubes vary in different species of plants, depending upon the lengths of the styles, through which they must grow. In some flowers such as those of willow and beet, the styles are only $\frac{1}{10}-\frac{1}{20}$ of an inch long and the pollen tubes are correspondingly short. In some lilies, the styles are 5 inches long and in the pistillate flowers of corn, the styles (silks) are frequently 16 to 20 inches long, with pollen tubes necessarily somewhat longer. In many short-styled flowers, only a few hours are required for the complete growth of pollen tubes, whereas in long-styled species, several weeks or months are usually needed for the attainment of maximum length of pollen tubes. The length of the style is not always a controlling factor in determining the time required for a pollen tube to complete its journey through the style; in oak flowers, for example, the pollen tubes require several months to grow through the styles which are usually not more than $\frac{1}{8}$ in. long, whereas in corn, the pollen tubes often complete their growth through 12 to 20 inches of style within 36 hours. Obviously factors other than style length determine the time required for the pollen tubes to reach the ovaries. The numbers of pollen grains which may produce tubes on a stigma vary

in different species of plants; in some, such as lilies and Jimson weeds, several hundred pollen grains may reach a stigma and form an equal number of tubes.

The pollen tubes continue their downward growth through the style until they reach the ovary cavity, within which the ovules are

Fig. 164. Pollen grain with tube
A. Pollen grain.
B. Pollen tube.
C. Tube nucleus.
D. Sperm nuclei.
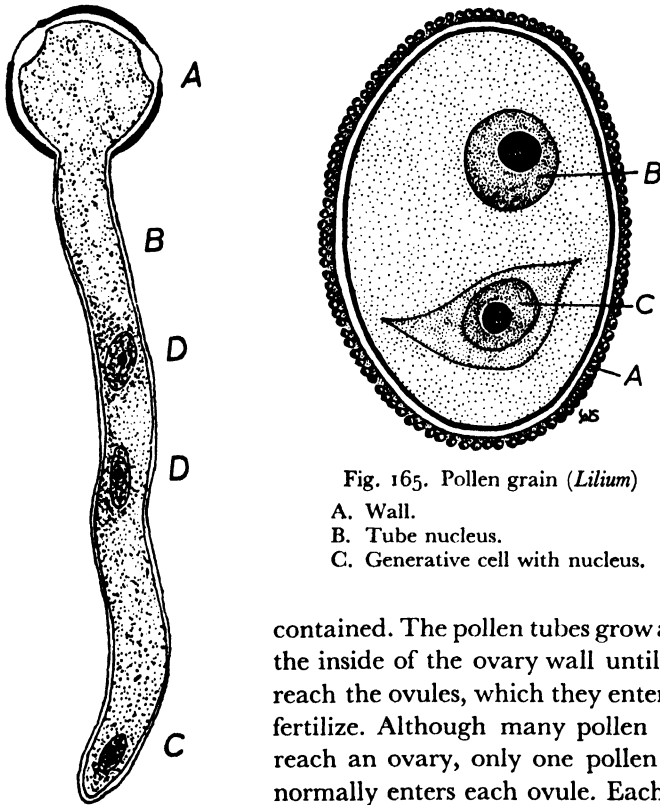
Fig. 165. Pollen grain (*Lilium*)
A. Wall.
B. Tube nucleus.
C. Generative cell with nucleus.

contained. The pollen tubes grow along the inside of the ovary wall until they reach the ovules, which they enter and fertilize. Although many pollen tubes reach an ovary, only one pollen tube normally enters each ovule. Each pollen grain contains two nuclei, a **tube nucleus** and a **generative nucleus**, and these enter the pollen tube when it is formed. The tube nucleus, which ordinarily precedes the generative nucleus in the growing tube, is not directly involved in fertilization, but controls the growth of the pollen tube. At some time during the development of the tube, usually early in its growth, the generative nucleus undergoes a single mitotic division, forming two **sperms**, or male nuclei, which are directly concerned with fertilization in the ovule.

As stated in the preceding section, a pistil is composed of one or more seed-bearing organs, or carpels. A carpel bears seeds along its margins which are turned inward longitudinally and fused along their line of meeting in a hollow, more or less cylindrical form. If the simple pistil (a single carpel) of a pea is opened along the line of marginal fusion and is spread out flat, it bears a striking resemblance in its form, venation, and color to a foliage leaf, from which it differs in that it has ovules, or undeveloped seeds attached to its edges. A carpel is regarded by many botanists as a leaf or as a structure similar in its development to leaves and engaged in reproductive rather than vegetative activities. In compound pistils, 2 or more carpels are fused together into one pistil. In some species such as lilies, there are as many cavities in the ovary of the compound pistil as there are carpels. In a lily ovary, there are three fused carpels, each fundamentally like the one-carpelled pistil of a pea, but combined into a single compound pistil with 3 separate cavities (one for each carpel) within which ovules are borne. In other species, such as orchids, which have 3-carpelled pistils, carpel fusion is such that there are no walls between the carpels; the ovary of such a pistil, though it is composed of 3 carpels, thus has but a single cavity within which the seeds are borne, usually in 3 groups. In most species of flowering plants, the number of styles or of style or stigma branches coincides with the number of carpels in their pistils and thus can be used as an index of carpel number. In lilies for example, there are 3 stigma branches and 3 carpels in a pistil, in cherry flowers 1 style and 1 carpel, in morning-glories, 2 style branches and 2 carpels, etc. There are some exceptions, however, to this correspondence; in a tomato flower, for example, there is a 2-carpelled, compound pistil, with a single, unbranched style.

An ovule, or undeveloped seed, is attached to the inside of the ovary in which it is borne by a short stalk (Figure 168). The outer cells of an ovule form one or two fairly distinct layers termed **integuments,** which become after fertilization the **seed coat** of the seed which develops from the ovule. At one end of an ovule, there is a tiny pore, called the **micropyle,** in the integuments. Inside the integuments and other outer cells of an ovule is a somewhat ovoid **embryo sac** (Figure 166), which usually occupies the greater part of the volume of an ovule. In a typical embryo sac, at the time when it is ready for fertilization, there are 8 nuclei — 3 at one end of the embryo sac, 3 at the opposite end, and 2 in the central region. Of the 3 nuclei nearest the micropyle one is an **egg,** or female nucleus. The 2 central nuclei are called **polar nuclei.**
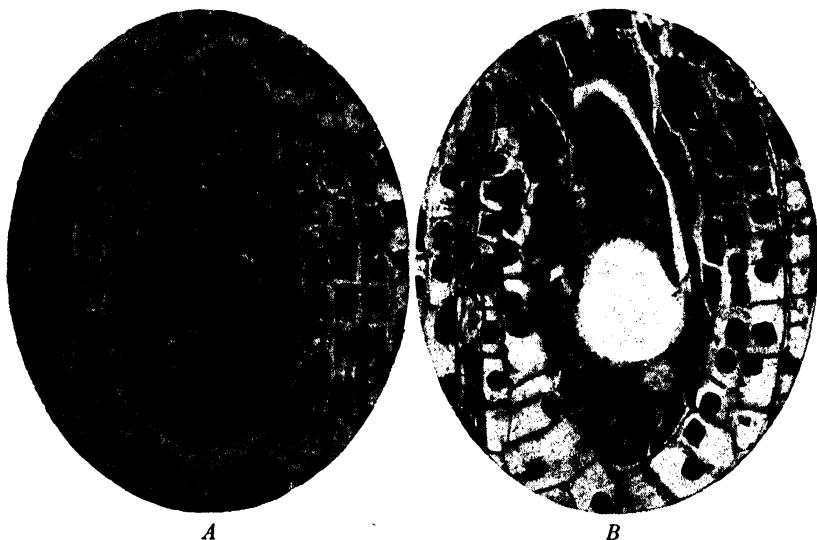
Fig. 166. Embryo-sacs of lily (*Lilium*).

A. Early stages with 4 nuclei.   B. Later stage, showing 6 nuclei.

When a pollen tube, after its journey down a style, reaches an ovule, it penetrates the micropyle and enters the embryo sac, into which it discharges a portion of its contents, most important of which are two **sperms**, or male nuclei. One of the sperms fuses with the egg in the embryo sac, a phenomenon termed **fertilization.** The other sperm fuses with the 2 polar nuclei of the embryo sac to form the **endosperm nucleus.** The process of the fusion of a sperm with the polar nuclei is often called triple fusion (Figure 167). The remaining 5 nuclei of the embryo sac usually disappear after the fertilization processes are consummated.

After the fertilization of the ovules, the ovary usually begins to enlarge into the **fruit** and as it does so, the ovules increase in size. The **zygote** (fertilized egg) by numerous cell divisions becomes the **embryo** of the seed. The endosperm nucleus grows into the **endosperm tissue** (the chief food storage tissue) of the seed. Simultaneously the integuments grow and harden to form the seed coat.

The complex series of events involved in pollination and fertilization are repeated in simple form for the purpose of review.

1. Pollen grains are transferred from a stamen to a stigma of the same flower, of another flower on the same plant, or of a flower on

Fig. 167. Longitudinal section of a complete, hypogynous flower, showing pollination and fertilization.

a. stigma.
b. style.
c. ovary.
d. pollen grain.
e. pollen tube.
f. ovule.
g. integuments of ovule.
h. ovule stalk.
i. embryo sac.
j. polar nuclei.
k. egg.
l. antipodals.
m. synergids.
n. micropyle.
o. tube nucleus.
p. sperms.
q. filament.
r. anther with pollen grains.
s. nectar glands.
t. petals.
u. sepals.
v. flower stalk.
w. vascular tissues.
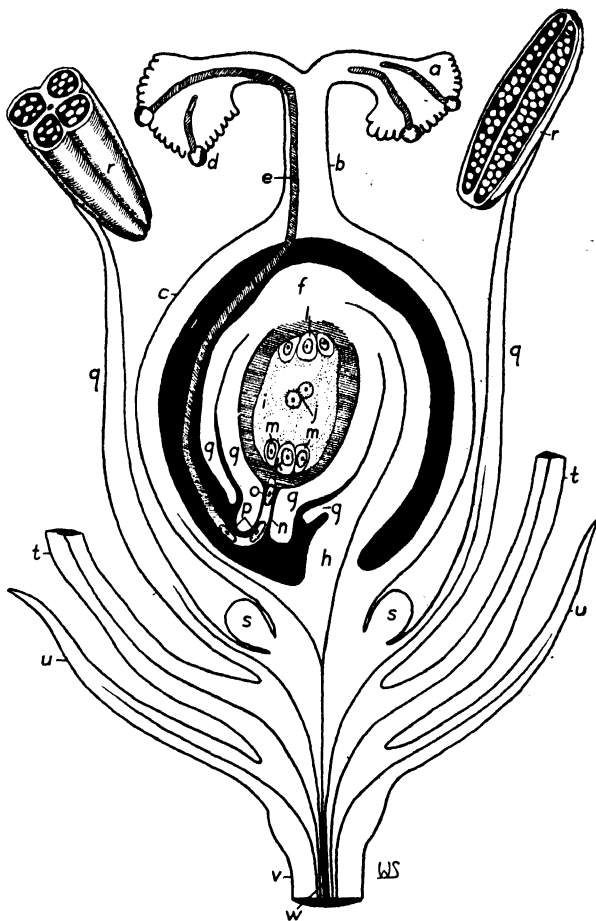
another plant of the same kind, by wind, insects, or some other agency (**pollination**).

2. Pollen grains on the stigma take up water from the stigma, swell, and form pollen tubes, which grow downward through the style.

3. Each pollen tube has a tube nucleus, which regulates the growth of the tube, and a generative nucleus, which divides once to form two sperms.

4. A pollen tube enters an ovule through the micropyle, a pore in the integuments of the ovule.

5. In an ovule there is an embryo sac, which at the time of fertilization contains 8 nuclei — 3 at the micropylar end of the embryo sac,

3 at the opposite end, and 2 (polar nuclei) in the central part of the embryo sac. One of the nuclei at the micropylar end is the egg.

6. A pollen tube entering the embryo sac of an ovule discharges its two sperms into the embryo sac.

7. One sperm fertilizes the egg, forming a zygote which by subsequent growth forms the embryo of the seed.

8. The other sperm fuses with the two polar nuclei, forming the endosperm nucleus, which after a period of numerous mitotic divisions gives rise to the endosperm or food storage tissue of the seed.

9. The integuments harden into the seed coat, the developing seed enlarges as a result of growth of the endosperm and embryo and the movement of food into it, and the fruit undergoes a simultaneous enlargement.

10. When the fruit reaches maturity, it splits open, or if there is no definite splitting, its walls disintegrate, and the now-mature seeds are freed.

The enlargement of ovaries into fruits and of ovules into seeds requires much food. Soluble foods, such as sugars, amino-acids, simple proteins, and fatty materials, move

Fig. 168. Section of lily ovary

A. Ovary wall.   C. Locule.
B. Ovary partition.   D. Ovule.

rapidly through the vascular tissues which connect flower parts with stems into the cells of the ovules and of the ovary walls. When these foods reach their destinations, they are converted usually into insoluble storage foods such as starches, fats, etc. In this process, the water content of maturing ovules and often of fruits decreases markedly, so that mature seeds contain a low percentage, usually not more than 10 or 12, of moisture. Seeds usually enter into a period of **dormancy,** or low physiological activity, until internal and external conditions become favorable for their germination. The development of seeds and fruits requires so much food that the entire food reserves of some plants are frequently exhausted, in which case death occurs.

This is a common phenomenon in annual plants, at the end of the second season's growth in biennials, and less frequently in such perennials as century plants (*Agaves*). As the ovary enlarges the stamens, petals, and often the sepals wither and fall. In some fruits, such as peas, the sepals persist and are found at the base of the matured seed pod.

As a rule, the development of ovules into seeds and the enlargement of an ovary into a fruit follow only after pollination and fertilization have occurred. In most species of flowering plants, the failure of pollination to occur results in a failure of fruit and seed formation. This phenomenon frequently occurs in nature. In many kinds of fruit trees, if heavy rains fall during the time when pollen is mature, the pollen grains are washed out of the flowers and as a consequence few or no flowers "set" fruits. When *Yucca* plants are grown in regions where *Yucca*-moths are not present, no fruits or seeds develop, for no pollination nor fertilization of ovules occurs. In a few species of plants, dandelions, for example, embryos often develop without fertilization, a condition known as **parthenogenesis.** Such seeds are frequently capable of germination and growth. In navel oranges, bananas, pineapples, and certain other species, ovaries often develop into fruits in the absence of pollination and fertilization. This type of fruit development is termed **parthenocarpy.**

SUMMARY

1. The characteristic reproductive structures of angiosperms are flowers.

2. A flower is interpreted morphologically as a reproductive shoot, bearing structures probably similar to leaves in their origin and development.

3. A complete flower consists of a receptacle, to which are attached 4 kinds of floral organs — namely, sepals (calyx), petals (corolla), stamens, and carpel(s) (pistil(s)). A pistil is made up of one or more carpels; the enlarged base of a pistil is termed the ovary and contains ovules, which develop into seeds after fertilization.

4. Sepals protect the inner parts of young flowers, petals attract insects, stamens produce pollen grains, and carpels produce ovules which eventually become seeds.

5. There are many variations in the structural and physiological features of flowers — numbers of parts, size and form of parts, color

kinds of parts present, presence or absence of odoriferous substances, nectar, etc., position of ovary, etc.

6. Flowers develop from buds, the floral organs arising as lateral protuberances of the growing points of buds.

7. A flower cluster is termed an inflorescence.

8. Pollination is the transfer of pollen grains from the stamens of a flower to the stigma of the same or another flower. The transfer of pollen from a stamen of a flower to the stigma of the same flower or to the stigma of another flower on the same plant is termed self-pollination. The transfer of pollen from a stamen to the stigma of a flower on another plant is termed cross-pollination.

9. Pollination is brought about mainly by insects and wind, to a lesser extent by water, birds, and other agents.

10. Many kinds of flowers have specialized mechanisms or modes of behavior which attract insects or increase the effectiveness of insect pollination.

11. Fundamental structural differences occur between wind-pollinated and insect-pollinated flowers.

12. The events which occur from the time of pollination through fertilization and the development of seeds are presented in brief form in section 4 of this chapter.

13. A fruit is a matured ovary, a seed is a matured ovule.

14. When seeds are released from the fruits in which they developed, they are often not capable of sprouting immediately but require a resting or dormant period, during which certain changes occur within the seeds.

15. The development of embryos in seeds without fertilization is termed parthenogenesis. The enlargement of a fruit without fertilization of its enclosed ovules is termed parthenocarpy.

Fruit and Seed Structure; Seed Germination; Economic Importance of Seeds

1. FRUIT STRUCTURE

AS DESCRIBED in the preceding chapter, a **fruit** is a matured **ovary** and a **seed** is a matured **ovule**, which is produced inside a fruit. The term fruit in its technical botanical sense is thus any kind of ripened ovary within which seeds are formed, and includes such diverse structures as bean and pea pods, bananas, grapes, peaches, okra, corn grains, apricots, tomatoes, dandelion "seeds," cucumbers, and watermelons. The popular usage of "fruit" differs somewhat from the botanical usage, in that it refers only to matured ovaries which are sweet and more or less pulpy. According to this popular definition, only bananas, grapes, peaches, apricots, and watermelons of the above list are fruits; beans and pea pods, okra, corn, tomatoes and cucumbers are popularly termed "vegetables," although botanically they are ripened ovaries or fruits, just as are grapes, peaches, etc. The term "vegetable" has only a popular significance and is used in this sense to designate plant parts, regardless of their structural nature, which are not sweet and which are usually flavored before they are eaten with salt, pepper, or other condiments. Thus, popularly, lettuce, spinach, potatoes, corn, string beans, and tomatoes are vegetables; botanically, lettuce and spinach are leaves, potatoes are tubers, and corn, string beans, and tomatoes are fruits.

In most plants, the fruits consist entirely of ovary tissue; such fruits are called **true fruits.** There are many kinds of fruits, which differ among themselves in size, the number of ovules which they contain, color, surface texture, shape, succulence, etc. The true fruits are generally grouped into 2 main classifications: **fleshy** (Figure 169) and **dry fruits.** Fleshy fruits are those in which the ovaries become entirely or partly soft and pulpy at maturity. The commonest types of fleshy
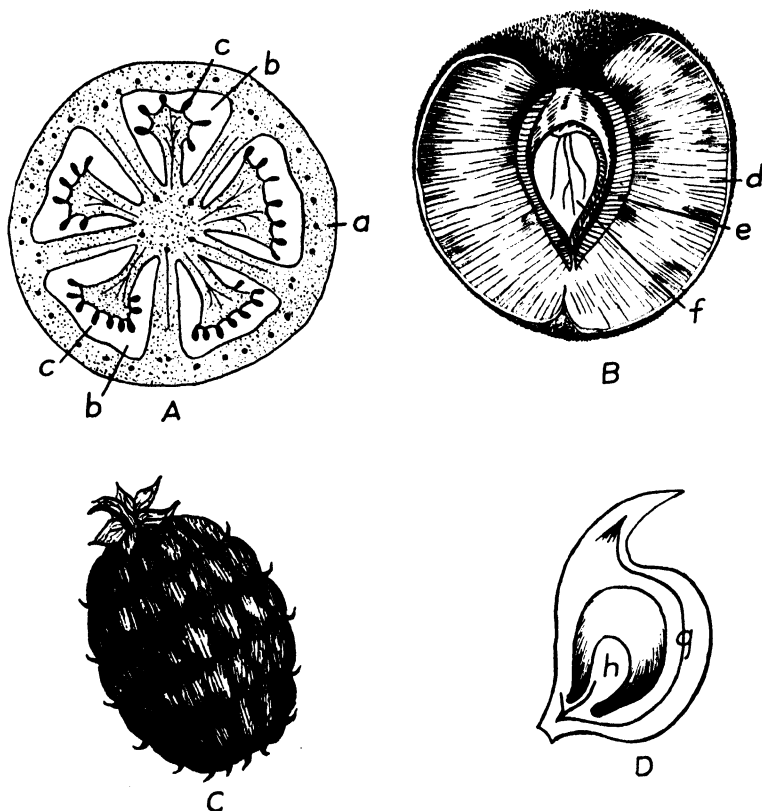
Fig. 169. Common types of fruits

A. Berry (tomato): a. pericarp, b. locules, c. seeds.
B. Drupe (peach): d. fleshy exocarp, e. endocarp (stone), f. seed.
C. Aggregate fruit of raspberry. Each division is a tiny drupe, developed from a single one of the numerous ovaries of a raspberry flower.
D. An achene of buttercup: g. pericarp, h. seed.

fruits are **berries** (grapes, tomatoes, bananas, watermelons, oranges), the entire ovary walls of which become pulpy, and **drupes** (peaches, plums, olives), in which the inner portions of the ovary walls become hardened ("pits"), and the outer wall layers become pulpy. Within the "pits" are produced one or two seeds. When the pulpy portions of fleshy fruits disintegrate, the pits are exposed.

In dry fruits (Figure 171), the ovary walls do not become soft but lose their moisture and become papery, chaffy, or very hard at maturity. Among the common types of dry fruits are **achenes** (Figure 175)

(buttercup, dandelion, sunflower) and **grains** (corn, wheat, oats), in both types of which a mature fruit contains but one seed. In **nuts,** which are also one-seeded, the ovary walls become much thickened and hardened at maturity. Common among many-seeded dry fruits are **legumes** (Figure 170), dry, single-carpelled fruits which split along two margins (peas, beans), and **capsules,** which develop from pistils composed of more than one carpel (snapdragon, iris, poppy).

In some species of plants, parts other than ovaries adhere to or enclose the mature ovaries. Fruits of this type are called **accessory fruits.** Among familiar accessory fruits are strawberry fruits, in which the individual fruits are achenes, borne upon a sweet, fleshy receptacle (the edible portion). Another common type of accessory fruit is a **pome** (Figure 173), exemplified by apples, pears, and quinces, in which the ovaries (sections of the core) are surrounded by enlarged receptacle and calyx tissues in which large quantities of food and water are stored. In pomes the true fruits (ripened ovaries) constitute the cores, which are not eaten. Thus, in strawberries, apples, pears, etc., the edible portions are not the ma-

Fig. 170. Opened bean pod
A. Fruit stalk.
B. Fruit wall (pericarp).
C. Seed.
D. Seed stalk.
E. Impression of seed.

tured ovaries, but stem and calyx tissues, in which or upon which the ovaries or true fruits are imbedded.

Fruits are sometimes classified upon the basis of the numbers and origin of the ovaries present in them. In blackberries and raspberries, the so-called fruit is really a cluster of separate, matured ovaries, each of which develops from one of the numerous simple pistils of a *single* raspberry or blackberry flower. Such a fruit-cluster is termed an

Fig. 171. The caryopsis. A. Longitudinal section through fruit of wheat (*Triticum sativum*). B. External view of wheat fruit. C. Longitudinal section through corn fruit. D. External view of corn fruit. E. Immature ear of corn, showing early stages in the development of the caryopsis.
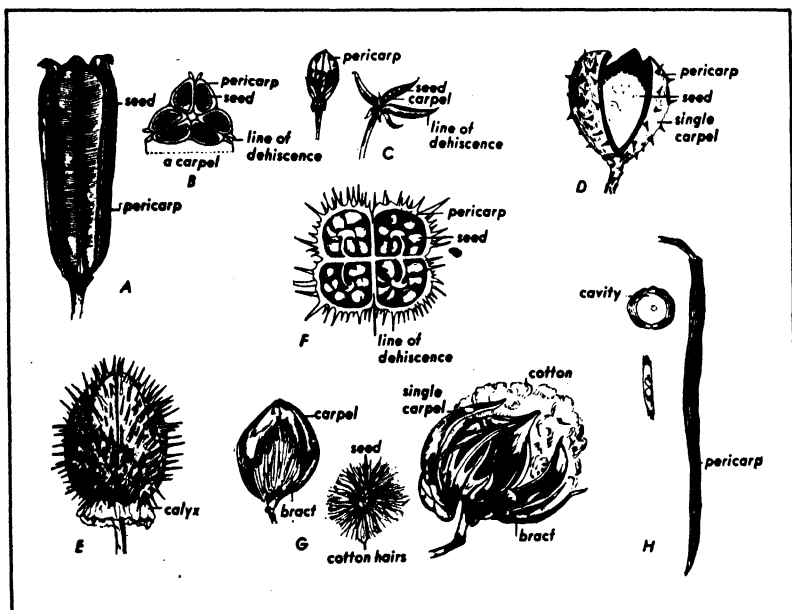
Capsules. A. Capsule of tulip. B. Cross-section of capsule of tulip. C. Mature capsule of pansy. D. Capsule of horse-chestnut (*Aesculus hippocastanum*). E. Spiny capsule of Jimson weed (*Datura stramonium*). F. Cross-section of capsule of Jimson weed. G. Capsule and seed of cotton (*Gossypium barbadense*). H. Entire capsule, cross-section, and seed of the Indian bean (*Catalpa bignonioides*).
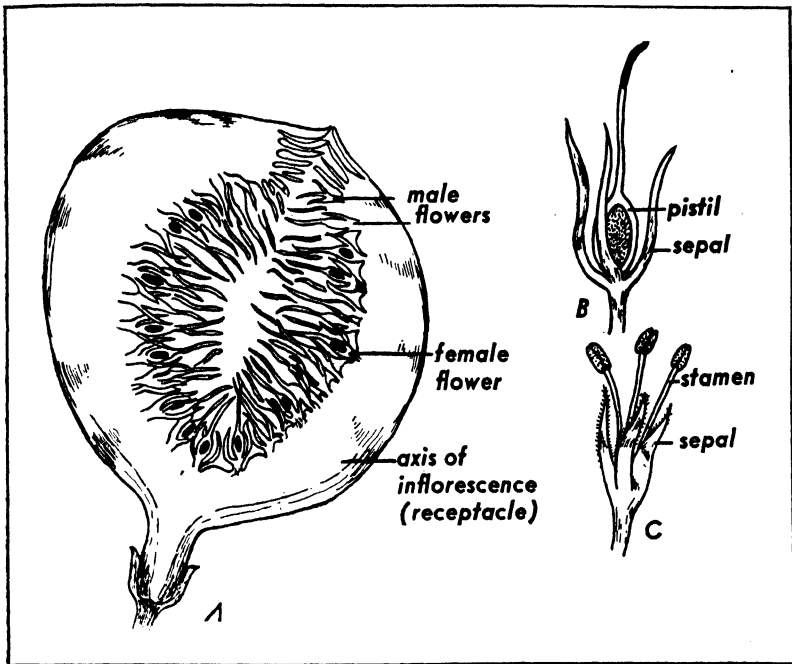
Fig. 172. Flowers and fruit of the fig. A. Fruit in longitudinal section. B. Female flower. C. Male flower.

Fruit of pineapple (*Ananas sativa*).

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Fig. 173. The apple is a pome (accessory) fruit

A. Peduncle.
B. Remnants of calyx and stamens.
C. Receptacle and calyx tissue.
D. Pericarp.
E. Seed.
F. Vascular bundles.
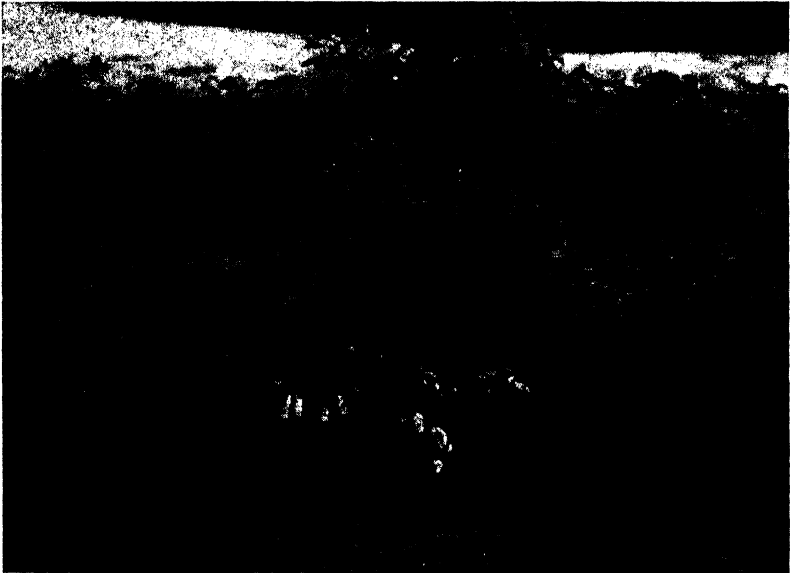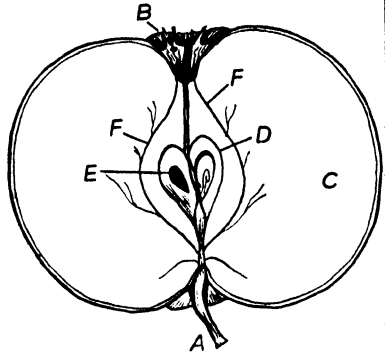
Photo by Missouri Botanical Garden

Fig. 174. Peanut plant showing the fruits, which develop underground after the flowers, which are borne and pollinated above the soil, bend downward, burying the young fruits.

Fig. 175. Fruit clusters of *Magnolia*, a rather primitive modern angiosperm. Each cluster is composed of the numerous, matured, separate achenes of a single flower.

aggregate fruit. Each of the individual fruits of a raspberry and a blackberry is a drupe; thus the name "berry" is entirely inappropriate to these fruits. In mulberries, figs, and pineapple, the fruit-clusters are composed of the densely-packed, ripened ovaries of *separate* flowers; a cluster of this type is called a **multiple** or **compound fruit** (Figure 172). Those fruits which develop from a single pistil (tomato, bean, corn, peach, etc.) are termed **simple fruits** to distinguish them from aggregate and multiple fruits.

2. SEED STRUCTURE

A seed consists essentially of a miniature, undeveloped plant (**embryo**), surrounded by a quantity of stored food available for its early nourishment, and a protective coat. All mature seeds capable of **germination** (sprouting) have embryos and **seed coats** (Figure 176). In every young developing seed, there is, in addition to an embryo and a seed coat, **endosperm,** or food storage tissue, which either before or during seed germination is digested and absorbed by the embryo. In the seeds of beans, peas, peanuts, sunflowers, pumpkins, and other species

of plants, the food stored in the endosperm tissue is absorbed by the embryo before these seeds leave their parent plants. Thus, when such seeds are mature they consist only of embryos and seed coats. In many other species, such as corn, castor bean, oats, and wheat, the digestion and absorption of the endosperm foods by the embryos do not occur until after the seeds are planted and begin to absorb water. In each of such seeds, then, there are present at maturity an embryo, a seed coat, and endosperm. Seeds of this type generally germinate slowly, for their embryos must remove food from the endosperm before they can begin vigorous growth. Beans, peas, and other seeds the embryos of which absorb the foods stored in the endosperm tissues before the seeds are mature generally germinate more quickly, for the preliminary step of food transfer from endosperm to embryos is completed before the seeds are planted.

As stated in the preceding chapter, a seed coat develops from the surface layers (**integuments**) of ovules. In some seeds there are present a tough, outer coat and a thin, inner coat; in others, only a single coat is present. Seed coats in most species of plants are rather tough and often partially waterproofed. Seed coats reduce the amount of water evaporation from the internal tissues and also afford protection against the entry of parasites, against mechanical injury, and, in some species, possibly against unfavorably high and low temperatures. There usually appears on a seed coat a small scar, known as the **hilum,** which marks the place of attachment of the seed to the seed stalk. Also apparent on the surface of many kinds of seeds is the **micropyle,** the pore through which the pollen-grain entered the ovule prior to fertilization. In some species, such as garden beans, the micropyle is distinctly visible at maturity, whereas in other species, the micropyle is obscured by the post-fertilization growth of the integuments.

An embryo consists of one or two (often more in gymnosperm seeds) **cotyledons, or seed leaves** and a somewhat elongated axis from which the cotyledons grow out. The portion of the axis above the point of attachment of the cotyledons is called the **epicotyl** (sometimes termed the **plumule**), that below the attachment of the cotyledons, the **hypocotyl,** the lower end of which is the **root-primordium** or **radicle.** The cotyledons are structurally leaves which function primarily in the digestion, absorption, and storage of food from the endosperm which surrounds or lies adjacent to the embryo in seeds. Because of their specialized functions, cotyledons rarely resemble the mature leaves of the plants of which they are parts. In some species, such as castor
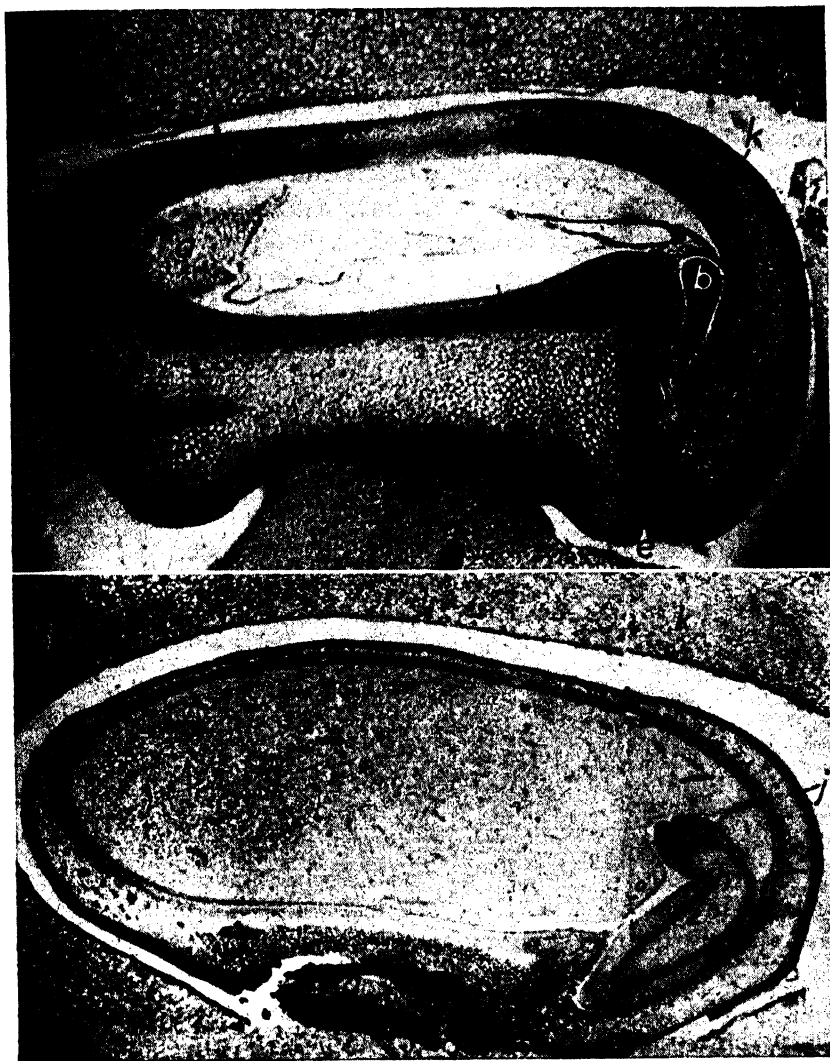
Fig. 176. Development of seeds of garden bean

A. Seed with young embryo
   a. endosperm.
   b. embryo.
   c. seed stalk.
   e. micropyle.
   f. ovary tissue.
   k. seed coat.

B. Later stage in bean seed development
   g. endosperm tissue.
   h. embryo: 1. epicotyl, 2. hypocotyl, 3. radicle.
   i. seed stalk.
   j. seed coat.
   k. ovary tissue.

beans, the flat, broad cotyledons persist for several weeks after germination and become green and photosynthetic. In garden beans, on the contrary, the fleshy cotyledons wither and fall off within a few days after germination. As stated in an earlier chapter, the angiosperms are subdivided into **monocotyledons** and **dicotyledons** on the basis of the number of the cotyledons in their seeds.

The hypocotyl, the portion of the embryo axis below the cotyledons, is a very short stem; at the lower end of the hypocotyl is the meri-
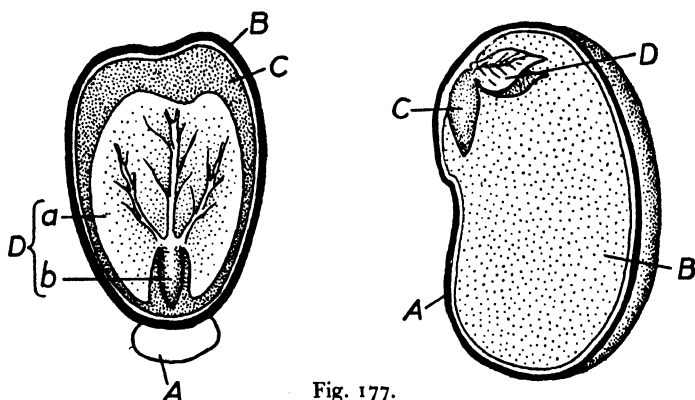
Fig. 177.

I. Longitudinal section of a
castor-bean seed

   A. Caruncle.
   B. Seed coat.
   C. Endosperm.
   D. Embryo: a. cotyledon,
      b. hypocotyl.

II. Longitudinal section of a
garden bean seed

   A. Seed coat.
   B. Cotyledon.
   C. Hypocotyl.
   D. Epicotyl.

stematic radicle, which develops into the primary root of the seedling. The epicotyl, the part of the embryo axis above the cotyledons, grows into all or most of the shoot system of the new plant. Both hypocotyl and epicotyl are composed chiefly or in part of meristematic cells which make possible the development of roots and shoots respectively from these parts of the embryo axis.

The endosperm tissue develops as a result of the fusion of a sperm with two polar nuclei in the embryo sac. It contains in its cells large amounts of usually insoluble stored food, which is withdrawn by the embryo before or during seed germination, as described earlier in this section. Carbohydrates are stored in large quantities in the seeds of many plants, chiefly as starches (corn, wheat, rice, beans), less frequently as sugars (peas, sweet corn) and occasionally as hemicellu-

lose. Carbohydrates serve chiefly as sources of energy for growth, in part for the structural material (cellulose) for cell-wall formation. Proteins are stored in all seeds; they are used chiefly in the formation of new protoplasm as germination begins and continues. In some seeds, such as those of dent corn, peas, beans, and soy-beans, very large quantities of proteins occur. Fats and oils are reserve foods, used primarily for energy, in the seeds of many species of plants. Seeds which are exceptionally rich in fats and oils are castor beans, peanuts, flax, coconut, sunflower, and soy-beans. In some plants, such as lilies, and tulips, no starch whatsoever is present. The chief energy foods in the seeds of these species are oils. In all seeds with insoluble stored foods, digestion is a preliminary phase of germination, for only those foods which are water-soluble can be translocated, readily respired, and assimilated.

Typical examples of common kinds of seeds in angiosperms are the seeds of garden beans, corn, and castor bean. Garden beans and castor bean seeds are dicotyledonous (Figure 177), corn is monocotyledonous (Figure 178). No endosperm is present in the mature seeds of garden beans; both corn and castor bean seeds

Fig. 178. Longitudinal section of a corn grain, a one-seeded fruit

A. Grain coat (pericarp and seed coat).
B. Endosperm.
C. Embryo: a. epicotyl, b. cotyledon, c. hypocotyl.
D. Grain stalk.

have abundant endosperm in their matured condition. The cotyledon in a corn grain is a small, shield-shaped structure (sometimes called a scutellum), whereas in beans and castor beans the cotyledons are respectively leaf-like and kidney-shaped.

3. SEED GERMINATION

In most species of plants, seeds require a period of relative rest or **dormancy** before they are able to germinate. This dormant period is advantageous to seeds, particularly in temperate zones, for dormant seeds remain in a condition of low physiological activity during the winter when low temperatures might kill seeds in an active state of germination or post-germination growth. Seeds may thus be regarded, in some degree at least, as structures which are able to carry a species safely through a period of unfavorable environmental conditions which might be fatal to physiologically active plant tissues.

The causes of seed dormancy vary in different species of plants. Seed coats are frequently too thick for the absorption of adequate quantities of oxygen or water. In such cases, germination does not occur until the seed coats have been weakened or cracked by natural forces such as bacterial action, freezing and thawing, etc. or by artificial scratching of the seed coats (**seed scarification**). Many agriculturally important seeds (e.g., sweet clovers and other members of the legume family) have seed coats which are very hard and which retard the entry of water. Various seed-scarifying machines, equipped with abrasive devices, are used to scratch or nick the coats of such seeds, which, after this treatment, absorb water readily and germinate quickly. In some species, the embryos of seeds are not fully developed at the time when the seeds are shed from the fruits; in such cases, a period of dormancy occurs during which the maturation of these embryos is completed. In other species, certain chemical changes must be completed before the embryos are capable of germination. Regardless of its cause, dormancy is always accompanied by a marked reduction in the water content of seed tissues, frequently to 4 or 5%. Cells with such low water content are much less susceptible to unfavorable external conditions than are physiologically active tissues with 75–90% water content.

Different kinds of seeds retain their **viability** (ability to germinate) for varying periods of time. The seeds of certain orchids and willows remain viable for *only a few days or weeks*, while those of the Indian lotus have been reported to retain their ability to germinate for approximately 250 years. In most species of plants, the periods of seed viability do not exceed three or four years. Sensational newspaper accounts of the growth of seeds from tombs of ancient Egyptian kings are falsehoods; no reputable botanist has ever found seeds of such great age to be viable. Although each species of plant has a characteristic viable

period, the length of this period is affected in part by storage conditions. Seeds stored in cool, dry places generally retain their viability longer than those exposed to warm, humid air. Many kinds of seeds might be kept viable for very long periods of time if proper conditions for their storage were known.

The completion of the dormant period, the age of a seed, the amount of auxins or substances capable of transformation into auxins, and the amount of stored food available are chief among the internal factors which influence the percentage and rate of seed germination. There are also many factors of the external environment which exert marked effects upon the sprouting and early growth of seeds. Most important of these external influences are moisture, temperature, and oxygen. Abundant water must be available for seed germination; the early stages of germination result in a tremendous increase (from approximately 25 to 200%) in the volume of seeds, an increase attributable principally to water intake. If water is present in such large quantities that oxygen is reduced or excluded, seeds frequently rot, for they are unable to respire normally and they are often attacked by anaerobic fungi which thrive in low concentrations of oxygen. Thus, seeds often rot in water-logged soils, particularly those of the clay type which holds water very tenaciously. On the contrary, seeds of some plants (e.g., some species of water lilies, cattails, etc.) germinate more rapidly under water or in water-soaked soils than they do under conditions of moderate moisture in the substratum. The temperature requirements for the complete and rapid germination of seeds usually coincide with the temperature requirements for the growth of active plant organs. Seeds of different species vary widely in their minimum, maximum, and optimum temperature requirements for germination.

When seeds absorb water, the digestion of stored foods begins, the rate of respiration increases rapidly, and the assimilation of foods into living protoplasm in meristematic regions begins. The amount of stored food decreases as digestion and respiration continue; sprouted seeds usually have smaller dry weights than ungerminated seeds largely because of the utilization of some of the stored foods in respiration. The energy released by respiration is used chiefly in assimilation, mitosis and other phases of growth; some of this energy is radiated as heat from germinating seeds and can be measured by suitable thermometers. With the absorption of water, the release of energy, and the inception of growth processes, the embryo becomes too large for the seed coat. Splits appear in the coat and the root-forming tip of the

hypocotyl emerges (Figure 181). The emergence of the young root be-
fore other parts of the embryo is distinctly advantageous, for a root
system which anchors the seedling and absorbs water and minerals is
thus established before the epicotyl begins its rapid development into
the shoot system. When the epicotyl com-
mences its activities, the primary root and
a few secondary roots are supplying to the
embryo the large amounts of water needed
for subsequent growth of the embryo.
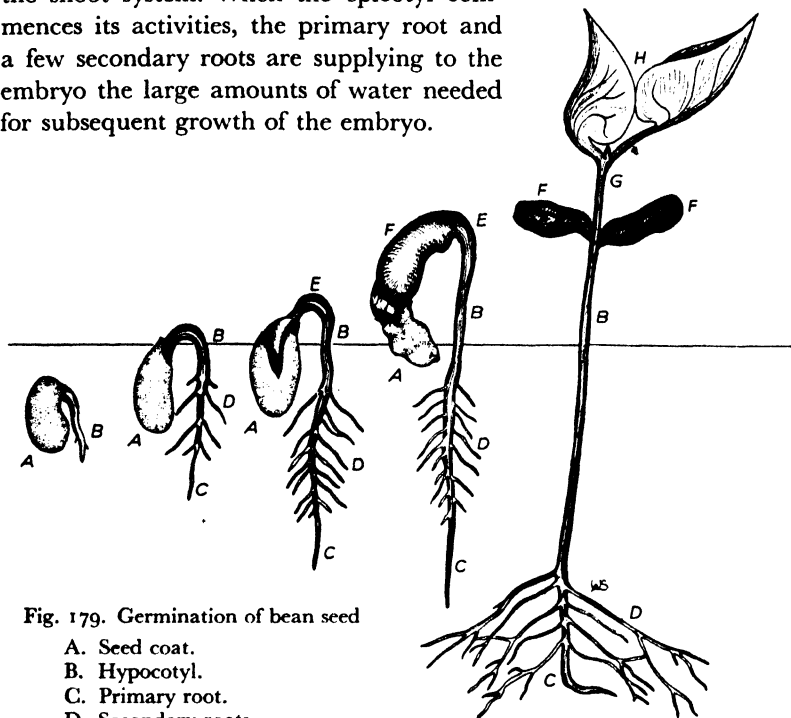
Fig. 179. Germination of bean seed.
  A. Seed coat.
  B. Hypocotyl.
  C. Primary root.
  D. Secondary roots.
  E. Hypocotyl arch.   F. Cotyledons.   G. Epicotyl.   H. First leaves.

In some species of plants, such as garden peas and corn, the hypo-
cotyl and cotyledons remain in the soil; only the shoot, formed by the
growth of the epicotyl, appears above the surface of the soil. In other
species, such as garden beans (Figure 179), sunflowers, and castor
beans, the root primordium of the embryo forms the primary root, as
in the case of peas and corn (Figure 180), but the upper part of the
hypocotyl, instead of remaining below the soil, as it does in pea and
corn seedlings, grows above ground for several inches, carrying the
cotyledons above the soil. The upper part of the hypocotyl is frequently
arched during its growth upward through the soil and straightens out
after it has emerged into the air. The arch of the hypocotyl forces a

path through the soil, as a result of which the epicotyl and cotyledons are protected against injury by soil particles, for they are literally pulled up by the growing crook-shaped hypocotyl. They do not push their own way upward through the soil. In beans and castor beans, the lowermost part of the stem is hypocotyl, whereas the stems of peas and corn develop entirely from epicotyls, the hypocotyls remaining in the soil.
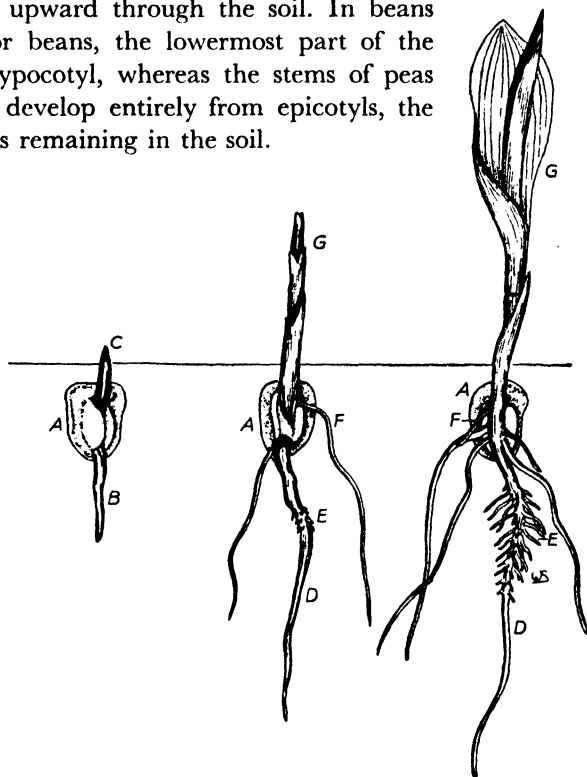
Fig. 180. Germination of corn grain

A. Grain.	E. Secondary roots.
B. Hypocotyl.	F. Adventitious roots.
C. Epicotyl (covered by epicotyl sheath).	G. Shoot.
D. Primary root.	

When the shoots have appeared above the soil, their growth and development continue as described in preceding chapters. In plants with dominant terminal buds, such as palms, the terminal bud of a mature tree is a direct descendant of the meristematic tissue of the epicotyl of the seed from which the tree grew. Likewise, in plants with dominant primary roots, the growing tip of the primary root is descended directly from the meristematic cells at the lower end of the hypocotyl of the embryo.
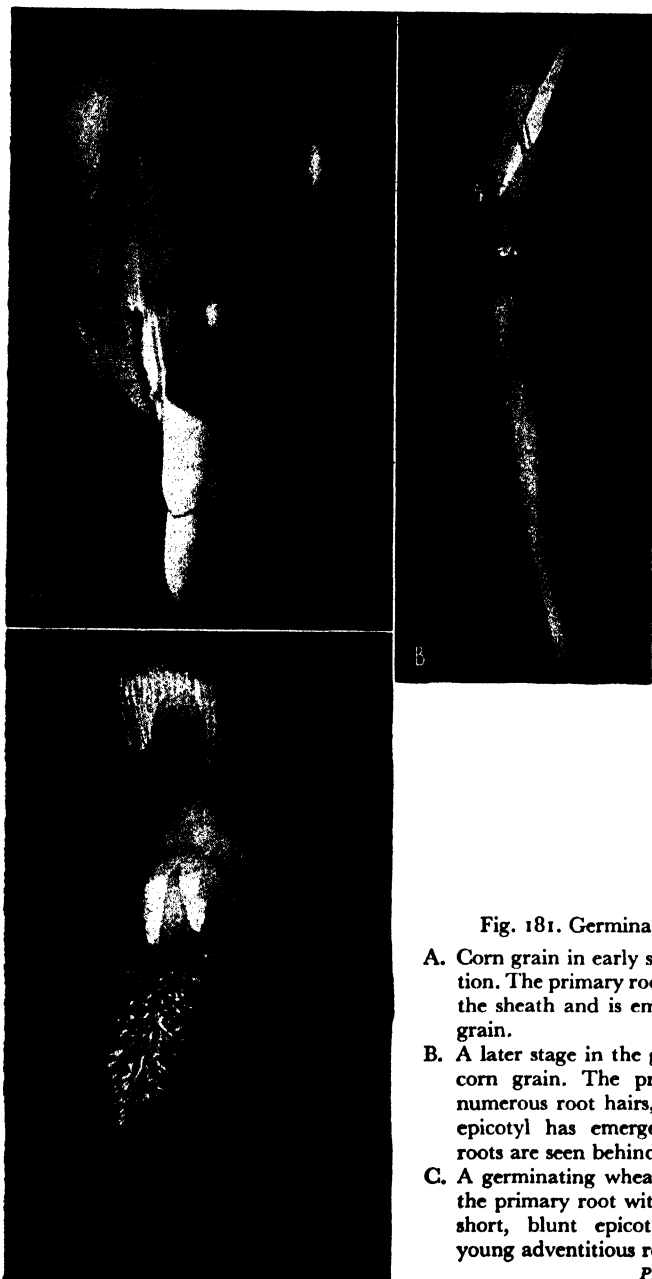
Fig. 181. Germinating grains

A. Corn grain in early stage of germination. The primary root has penetrated the sheath and is emerging from the grain.
B. A later stage in the germination of a corn grain. The primary root has numerous root hairs, and the plump epicotyl has emerged. Adventitious roots are seen behind the epicotyl.
C. A germinating wheat grain, showing the primary root with root hairs, the short, blunt epicotyl, and several young adventitious roots.

Photo by O. T. Bonnett

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Seeds are able to sprout and grow, often for several weeks, in darkness. This growth continues only so long as there is stored food available within the seedling for further growth and respiration. When all the food reserves are exhausted seedlings in darkness die. Continued growth beyond this point can occur only when the seedlings are illuminated and can thus carry on photosynthesis.

4. FRUIT AND SEED DISPERSAL (FIGURE 182)

Many kinds of plants have fruits or seeds which are equipped with special structures or peculiarities of behavior which increase the effec-

Witch hazel

Touch-me-not

Maple

Wafer ash

Linden

Sticktights

Spanish needles

Sweet cicely

Dandelion

Sycamore

Milkweed

Burdock
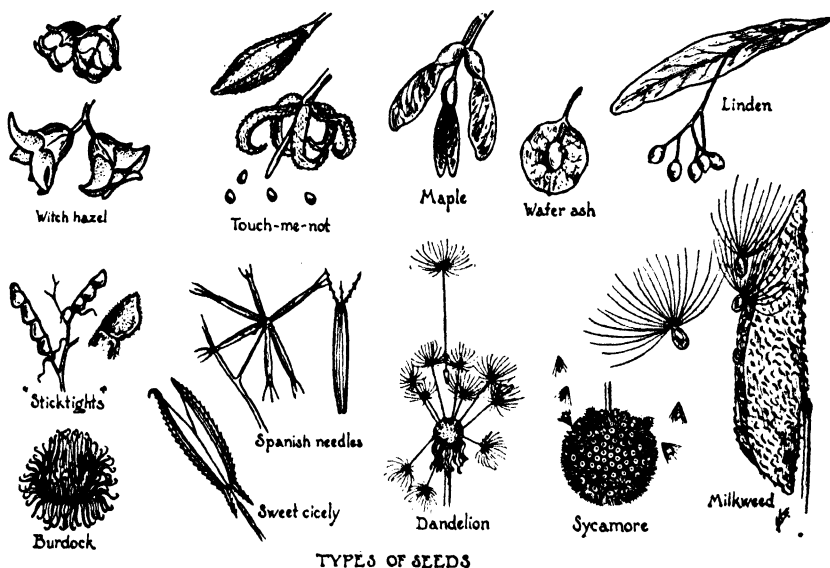
TYPES OF SEEDS

Fig. 182. Types of seed- and fruit-dispersal mechanisms.

tiveness of their spread, or **dispersal** over wide areas. Among the common dispersal mechanisms of seeds and fruits are:

1. *Wings* — such as those of elm, maple, and ash fruits, and catalpa seeds. These structures facilitate dispersal by wind.

2. *Plumes* — such as those of dandelion fruits and milkweed seeds. These seeds are likewise dispersed by wind.

3. *Spines* and *barbs* — such as those of the fruits of needle-grass, beggar's-tick, and wild carrot. These fruits are fastened by their spines to the fur of animals and to the clothes of human beings and are thus carried as "hitch-hikers."

4. *Air-spaces* or *corky floats* — these enable certain seeds and fruits to float on water and thus to travel for long distances in ocean currents. Curly dock fruits have corky ridges which enable them to float. Many seeds, such as those of some tropical legumes, have large amounts of air stored in them and are carried by ocean currents. Seeds of trees growing in the Orinoco river valley of South America, for example, are frequently cast upon the shores of the Scandinavian peninsula.

There are many other ways of less highly specialized nature by means of which fruits and seeds are dispersed. In touch-me-nots, sheep sorrel and sweet peas, the fruits explode at maturity, scattering the seeds as they do so. Plants with fleshy fruits which are eaten by birds are dispersed by the passage of their seeds through the alimentary canals of the birds. Russian thistle and tumbleweeds become detached from their roots when their seeds are mature and as they are rolled along the ground by winds they scatter their seeds. Squirrels transport and bury nuts, many of which are never reclaimed and which subsequently germinate. In many cases, minute seeds, such as those of orchids and foxgloves, are blown considerable distances by wind.

Man is one of the most important agents of seed dispersal. In his migrations he has carried with him to all parts of the world valuable crop plants and likewise, inadvertently, some of his most obnoxious weeds, such as goose grass, Russian thistle, and many others. A brief consideration of the original native distributions of several economically important plants illustrates how man has been instrumental in their dispersal:

Species	Place of Origin	Other Places Now Growing
Corn	Central America	Europe, Asia, U.S., West Indies, Africa, etc.
Bananas	Southeastern Asia	Tropics all over the world
Pineapple	South America	Hawaii, and many other parts of tropics
Wheat	Southwestern Asia	N. America, Europe, S. America, etc.
Hemp	Asia	World wide
Oats	Probably Asia	World wide
Breadfruit	Malaya	World tropics
Sugar cane	Southeastern Asia	North America, Asia, etc.
Quinine	South America	Java, Ceylon, Sumatra
Coffee	Abyssinia	World tropics
Para rubber	Brazil	India, Sumatra, Java, Africa, etc.

5. ECONOMIC IMPORTANCE OF SEEDS

Seeds are of fundamental importance to man because they constitute the chief method of propagation of the seed-plants, particularly annual and biennial species. Many seeds constitute man's most important food plants — for example, corn, wheat, rice, beans, peas, rye, oats, barley, peanuts, walnuts, pecans, almonds, and coconuts. Some furnish oils; the oils from coconuts, soy-beans, flax-seeds, tung, cotton, and corn are used as foods, in the manufacture of paints, varnishes, linoleum, lubricants, soaps, etc. Many seeds are used for the flavors which they impart to foods — anise, dill, caraway, nutmeg, mustard, etc. Some seeds furnish medicines — for example, castor beans, chaulmoogra (used in the treatment of leprosy), and psyllium. Seeds of coffee and cacao furnish important beverages. The hard hemicellulose material of the seeds of the ivory-nut palm furnishes a product called "vegetable ivory," used in the manufacture of buttons and as a substitute for ivory in inlays, chessmen, etc.

SUMMARY

1. A fruit is a matured ovary, a seed is a matured ovule.

2. A true fruit consists only of ovary tissues. An accessory fruit consists of ovary tissues, plus adhering or surrounding tissues derived from sepals, receptacle, or other flower parts.

3. Some of the more common kinds of true fruits are listed in this outline:

A. Fleshy fruits — the mature fruit is partly or wholly fleshy at maturity.

    a. Berries are entirely fleshy at maturity — e.g., tomato, grape.

    b. Drupes are fruits in which the inner part of the ovary wall becomes hard and forms a "stone," within which one or two seeds are borne, and the outer part of the ovary wall becomes soft and pulpy, e.g., peach, olive.

B. Dry fruits — the tissues of the fruit lose their moisture as they mature and become papery, chaffy, or very hard at maturity.

    a. Dehiscent dry fruits split open along definite seams.

        (1) Legumes are single-carpelled fruits which split along 2 seams — e.g., peas, beans.

        (2) Capsules develop from compound pistils and split along several seams — e.g., iris, tulip.

    b. Indehiscent dry fruits do not split open at maturity.

        (1) Achenes are small, one-seeded fruits in which the seed coat and fruit wall are separate — e.g., buttercup, sunflower.

(2) Grains are small, one-seeded fruits in which the seed coat and fruit wall are fused together — e.g., corn, wheat.

(3) Nuts are fruits in which the entire ovary wall becomes very hard. A nut contains one seed — e.g., hazel-nut, acorn.

4. Examples of accessory fruits are:

a. Strawberries, in which the true fruits are achenes embedded in the surface of an enlarged pulpy receptacle.

b. Apples and pears (pome fruits), in which the true fruits are the cores and the edible portions are enlarged receptacle tissues.

5. Fruits are often classified on the basis of the number of ovaries present and their origin:

a. A simple fruit develops from a single ovary.

b. An aggregate "fruit" is a cluster of matured ovaries borne in a single flower — e.g., raspberry, blackberry.

c. A multiple "fruit" is a cluster of matured ovaries from separate flowers on a common receptacle — e.g., Osage orange, pineapple.

6. A seed consists of:

a. A seed coat, primarily a protective structure, developed from the integuments of an ovule.

b. An embryo, or miniature plant, consisting of

(1) cotyledons (one or two in angiosperms) — food digesting and storing structures.

(2) epicotyl, a shoot-producing structure.

(3) hypocotyl.

(4) radicle, which develops into the primary root.

c. Endosperm, or food-storage tissue, developed from the fusion of a sperm nucleus with 2 polar nuclei in the embryo sac.

7. During or before seed germination, the cotyledon(s) digest and absorb the foods stored in the endosperm. This conversion of endosperm food into embryo tissue may occur before seeds leave the parent plants, as a result of which the mature seeds have no endosperm.

8. Most seeds must pass through a dormant period before they can germinate. Numerous causes of dormancy have been found.

9. The ability of seeds to remain alive and capable of germination is called viability.

10. When seeds germinate, they absorb large amounts of water, their embryos digest food, foods are respired, and assimilation and growth occur.

11. The primary root is usually the first structure to emerge from a germinating seed.

12. Many seeds and fruits have structural devices which facilitate their dispersal by animals, wind, and water.

Variation and Heredity in Plants; Plant Breeding

O NE OF the most striking qualities of living proto-plasm is its ability to beget protoplasm of the same kind. When a species of plant or animal reproduces, its offspring are always like their parents in their fundamental characters. Robins inevitably produce more robins, snapdragons always produce seeds which grow up into another generation of snapdragon plants. The tendency of progeny to resemble their parents in all fundamental features of structure and behavior is called **heredity.** All organisms inherit the characteristic attributes of their species from their parents. Not only are they recognizably members of the same species as their parents, but they often inherit certain peculiarities and thus resemble their parents more than they do other individuals of the same species. Despite the fact that all organisms are fundamentally like their parents, they usually differ from them in certain minor respects. No child is ever a perfect duplicate of his mother or father; he is a member of the human species, as are his parents, and he may show a marked resemblance to one or both of them, but he is at the same time an individual who is different, if ever so slightly, from them. White elms are all unmistakably white elms, yet each tree is an individual living organism which differs in some quality or other from all other white elms. This tendency of organisms to differ in slight degree from their parents is termed **variation.**

1. VARIATION

Variations within a certain plant or animal species are of three common types: **environmental modifications, mutations,** and **combinations.**

Plants of the same species often vary from each other because they are subjected to differences in environmental conditions. Plants grown in poor soils do not grow as large or produce as much food as plants

which grow in fertile soils. Plants exposed to bright sunlight manufacture more food than those growing in weak light and thus have greater dry weights and larger quantities of stored food. These differences caused by variations in available moisture, light, soil nutrients, and other environmental factors are not inherited, that is, they are not transmitted to the offspring of the plants subjected to the varying environmental conditions. The seeds of Bonny Best tomatoes, whether they are derived from tall plants grown in fertile soil or from runts grown in poor soil, usually produce plants of nearly the same quality if they are planted and allowed to grow under similar environmental conditions. The variations induced by environmental factors are thus not a part of the inheritance of a species and are limited in their extent and quality by the hereditary characteristics of a species. Good care and proper nutrition produce large healthy mice and oats; but no amount of solicitude or special treatment will ever transform a mouse into an elephant or an oat plant into a corn plant. Some biologists believe that differences in environmental conditions operating through long periods of time induce heritable changes in living organisms; such changes, if they occur, should not be confused with the modifications which are brought about in individual plants or animals by varying environmental conditions and which are not heritable.

Mutations are sudden, unpredictable changes which occur in organisms and which cannot be explained on the basis of environmental modification or cross-breeding. These changes are frequently insignificant, but in some cases are so marked that the offspring which arise by mutation often seem to be new varieties or species. Mutations are apparently caused by changes in the chromosomes or chromosomal constituents of mutating organisms or parts of organisms. The internal and external factors which cause mutations to appear in plants and animals are not well understood. The characters which develop by mutation are usually passed on by mutating organisms to their offspring; that is, they are heritable and persist from generation to generation as permanently established variations. Mutations occur in plants raised from seeds, or they may develop from individual buds on a stem. These are known respectively as **seed mutations** and **bud mutations.** In the case of a mutation which develops in a bud, the twig which grows from the bud differs in some manner from all other twigs of the plant. Many important varieties of cultivated plants have had their origins in mutations. Among these are navel oranges, certain varieties of Boston ferns, the weeping habit of willows, nectarines, many kinds of double-

flowered plants, Cuban tobacco, and certain sweet pea and chrysanthe-
mum varieties. Bud variations are usually propagated by bud-grafting
or other means of vegetative propagation.

The third type of variation, termed combination, occurs as a result
of the breeding of related, though somewhat different types of organ-
isms. This "crossing" of two varieties of a species or of two closely
related species often results in offspring with new characteristics.
Organisms which originate in this manner are called **hybrids,** and the
process of cross-breeding which results in their development is termed
hybridization. The phenomena involved in the formation of hybrids
and thus in the production of new variations are exceedingly complex.
The study of the scientific bases of hybridization is relatively new, its
origins dating back to the latter part of the nineteenth century. The
variations resulting from hybridization differ from environmental
modifications in that they are heritable and from mutations in that
they follow definite laws and can thus be produced and controlled
experimentally and frequently directed toward desired ends.

2. THE LAWS OF HEREDITY

The first of the fundamental laws which govern hereditary processes
were discovered by an Austrian monk, Gregor Mendel, who published
the results of his important experiments on inheritance in peas in 1866.
The great value of Mendel's experiments was not recognized until 1900,
some years after his death, when several geneticists (students of inherit-
ance) discovered the value of the experiments described in his short
publication. Mendel's work differed from that of his predecessors in
that he studied the inheritance of a single characteristic at one time, in-
stead of attempting to trace the inheritance of a number of traits
simultaneously, a task of infinite complexity and difficulty. Mendel
proceeded differently in another respect, in that he kept very accurate
records of the pedigrees of every plant with which he worked. Thus
he knew the parents, grandparents, great-grandparents and the more
remote ancestors of every individual plant involved in his breeding
experiments. Mendel established another precedent in the science of
heredity (**genetics**); he studied not only the *kinds* of variations which
developed from his cross-breeding experiments but also the *numbers* of
the various types of offspring produced. Thus his study was both
quantitative and *qualitative*, a fundamental feature of the scientific method
of investigation.

For his study, Mendel chose peas because they grow quickly from seed to maturity, thus producing many generations in rapid succession, and because their flowers are normally self-pollinated. The latter feature was an important one in his choice, for foreign pollen from unknown sources usually does not reach the stigmas of pea flowers and thus cannot introduce unknown factors into breeding experiments. In his first work, Mendel crossed types of peas which differed from each other in a single trait (**monohybrid** or **single-character crosses**). He crossed pea varieties which were alike in all respects, except that some were tall and some were dwarfs. He crossed varieties which were similar, except that some plants produced smooth seeds and others formed wrinkled seeds. He also crossed yellow-seeded peas with green-seeded peas, and white-flowered peas with colored-flowered peas, in all cases using for his experiments plants which differed in a single feature. In later experiments Mendel cross-bred types of peas which differed in two characters (**dihybrid** or **two-character crosses**). For example, he mated tall plants which formed smooth seeds with dwarf plants which produced wrinkled seeds.

Mendel, in performing his crosses, used the same methods employed at the present time. He removed the immature stamens from a flower which was to serve as the female parent, in order to prevent self-pollination, and placed on its stigma pollen from the flower to be used as the male parent. He then covered the hand-pollinated flowers to prevent foreign, unknown pollen from reaching the stigma and fertilizing the ovules. In such experiments, pollen from one variety, for example, a tall pea plant, is placed upon stigmas of the variety, a dwarf pea, with which the cross is being made. A reciprocal cross is also made, using pollen of the dwarf variety on stigmas of the tall variety.

Following such cross-pollination, the ovaries produce seeds. These seeds, when planted, grow into the first generation of offspring from the cross, termed the F_1, or **first filial generation**. The offspring of this generation, when self-pollinated, constitute the F_2, or **second filial generation**; the offspring of the F_2 are known as the F_3 generation, etc.

The first significant discovery by Mendel was the fact that in a cross between tall and dwarf peas, for example, all of the F_1 plants were tall, like the tall parent and that no dwarf plants appeared from the seeds produced by the cross (Figure 183). When these F_1 plants were self-pollinated, the F_2 generation consisted of *both* tall and dwarf plants, which resembled their grandparents. Mendel found a similar result in crosses between peas differing in other traits. For example, when
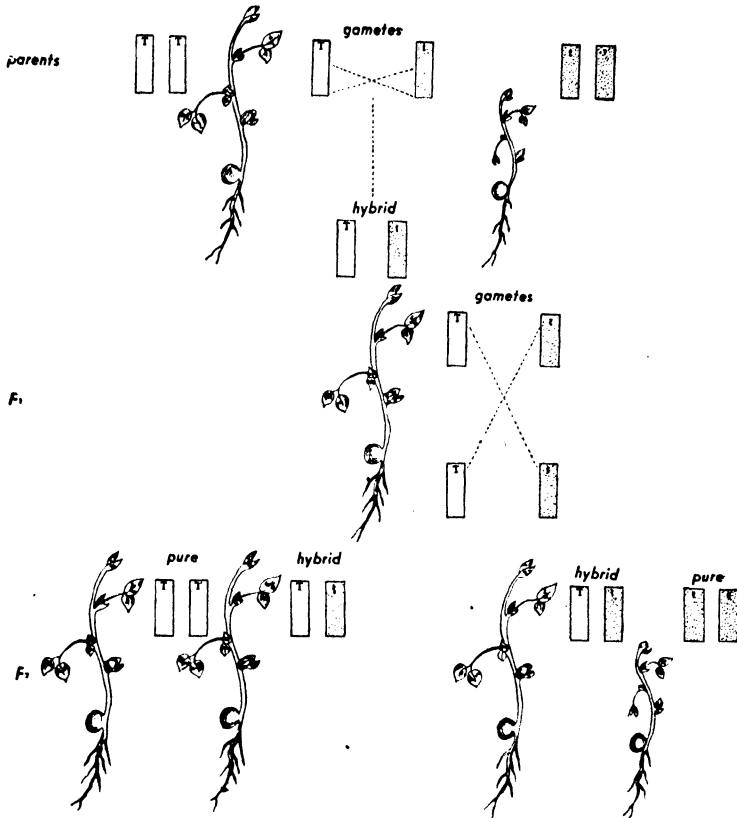
Fig. 183. An illustration of a simple Mendelian heredity when a pure-bred tall pea plant is crossed with a pure-bred dwarf plant. T in a chromosome represents a gene for tallness; t, a gene for dwarfness. Stippled chromosomes represent those derived from one parent; clear chromosomes, from the other parent. Only the chromosomes carrying genes involved have been shown. All others have been omitted.

smooth-seeded peas were crossed with wrinkled-seeded peas, all of the F_1 plants had smooth seeds, but the F_2 plants produced both smooth and wrinkled seeds. As a result of these discoveries, Mendel proposed the **law of dominance,** which states that when two contrasting characters are brought together in a cross as in a F_1 generation, one character frequently dominates and masks the other, which thus remains obscured. The character which dominates another is termed a **dominant** character; the character which is hidden is called the **recessive.** In peas, tallness is dominant over dwarfness, smooth seeds over wrinkled seeds, colored flowers over white flowers, green pods over yellow pods, etc.

F$_1$

F$_2$
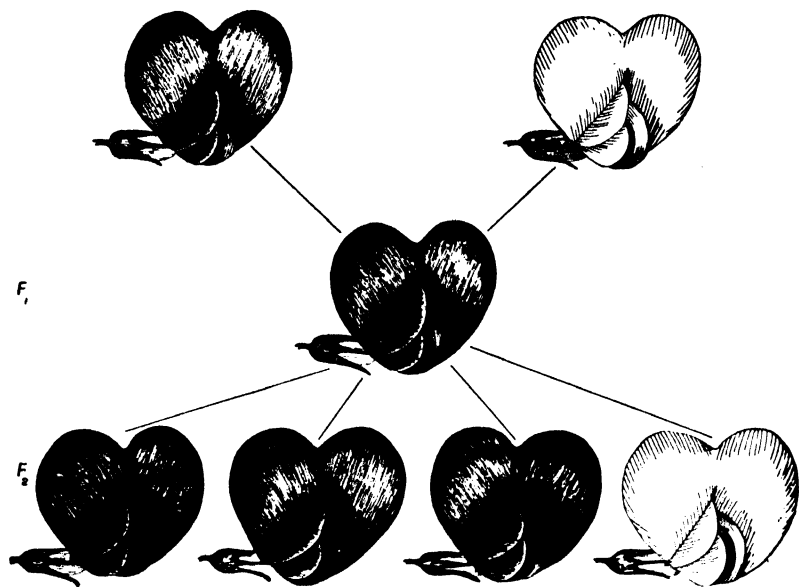
Fig. 184. Cross between a homozygous red-flowered and a homozygous white-flowered sweet pea. Red color is dominant over white. Notice that the F$_1$ flowers are all red and that the F$_2$ flowers are red and white, in the ratio of 3 : 1 respectively.

In the F$_2$ generations of such plants as peas, the dominant and recessive characters appear in a rather constant ratio of approximately 3 dominant plants to 1 recessive. Two of these dominant plants are **heterozygous**; that is, they are like the plants of the F$_1$ generation and produce, after self-fertilization, plants of both dominant and recessive types, again in the 3 : 1 ratio. The third plant with the dominant character in the F$_2$ generation is a **homozygous** (pure-line) dominant plant; that is, when it is self-pollinated, its offspring are all like itself both in appearance and in genetic constitution. The recessive plants, which constitute ¼ of the F$_2$ generation, are all homozygous plants which continue to produce recessive plants upon self-pollination. Mendel ascertained before beginning his hybridizing experiments that the parents used for crosses were homozygous; he knew that the variations appearing in the hybrids resulting from such crosses developed from ancestors which were genetically constant and which therefore did not carry hidden recessive characters which could have confused the results in the progeny of such crosses.

Dominance occurs in many types of crosses, but there are many cases of inheritance in which this phenomenon does not appear. In

such plants as snapdragons and four-o'clocks, the F_1 generations are usually intermediate between the parent types with respect to individual traits. For example, when homozygous red-flowered four-o'clocks are crossed with homozygous white-flowered four-o'clocks, the F_1 plants are pink-flowered (Figure 185). When the pink-flowered F_1 plants are self-pollinated, the plants of the F_2 generation are of three kinds: red-, pink-, and white-flowered, in the ratio of 1 : 2 : 1. The red- and white-flowered plants of the F_2 generation are homozygous, whereas the F_2 pink-flowered, like the F_1 plants, are

Fig. 185. Incomplete dominance in the crossing of four-o'clock flowers. Upper row: white and red parents when crossed produced white, magenta, and red offspring in the proportions as illustrated in the last row. (From Krecker, from Morgan, Sturtevant, Muller, and Bridges.)

heterozygous. This behavior is sometimes called **incomplete dominance.**

It is interesting to note that the 1 : 2 : 1 ratio in cases of incomplete dominance is fundamentally the same from the standpoint of genetic constitution (**genotype**) as the 3 : 1 ratio occurring in the F_2 generation in cases of complete dominance. The 3 : 1 ratio between the members of the F_2 generation of a single-character cross in which one character is dominant and the contrasting character is recessive, means that there are three plants with the dominant character to every one plant which shows the recessive character. Thus, on the basis of external appearance (**phenotype**), there are only two kinds of plants in the F_2 generation of such a cross. If the plants which show the dominant character are self-pollinated, it becomes apparent that only one third of them is homozygous (producing offspring of the same type); the other two thirds of these F_2 plants with the dominant character are like the F_1 plants in that they are heterozygous, producing two types of F_3 offspring, one kind showing the dominant character, the other the recessive, in the 3 : 1 ratio. The dominant plants of the F_2 are alike phenotypically because the dominant character masks the recessive in two thirds of these plants; genotypically, however, the dominant plants of the F_2 are of two kinds — one third of them is homozygous like its dominant, homozygous grandparent, the other two thirds are heterozygous like the plants of the F_1 generation. In four-o'clocks, the genotypic

and phenotypic ratios correspond because of the lack of complete dominance of one character over another; in peas, the genetic ratio differs from the appearance ratio because the dominant character masks the recessive characters in $\frac{2}{3}$ of the dominant individuals (Figure 183).

The most significant fact of dominance is that the appearance of an organism does not always indicate its ancestry or its hereditary constitution; plants may have the same appearance but may differ genetically, as shown by the diversity of offspring which they produce.

A second principle which Mendel stated was that embodied in the **law of segregation,** which states that in the offspring of heterozygous plants produced by a cross there is a separation or segregation of characters. Thus, in the F_1 generation of a cross between pure-line red and white four-o'clocks, all the plants are pink-flowered, but when the F_1 generation is self-pollinated, redness, whiteness and pinkness separate out in its offspring, the F_2 generation plants. This segregation of traits, or more properly, of the hereditary determiners of traits, occurs when a plant (or animal) forms sex cells or at some time prior to sex cell formation, as will be described later.

Mendel's study of the hereditary phenomena involved in crosses between peas differing in *two* traits led to his enunciation of the third principle or law of inheritance — the **law of independent assortment.** Mendel crossed, for example, homozygous yellow, round-seeded peas with green, wrinkled-seeded peas (Figure 186) and found that all of the plants in the F_1 generation produced yellow, round seeds, since yellowness and smoothness are dominant over greenness and wrinkledness. When these F_1 plants were self-fertilized, they produced offspring like the original pure-line parents — namely, plants which bore yellow, round peas, and green, wrinkled seeds — and *in addition*, two other kinds of seeds, in which these four characters had separated and had recombined. The plants of these two types produced yellow, wrinkled seeds and green, round seeds. Thus, two new combinations of characters were formed as a result of the cross-breeding of parents differing in two characters. Mendel found a rather constant mathematical ratio among these four types of seeds in the F_2 generation; there were approximately 9 yellow-round seeds to 3 yellow-wrinkled, 3 green-round, and 1 green-wrinkled seed. The seeds with both dominant characters were in greatest abundance, the two types with one dominant and one recessive character expressed were less frequent, and least numerous were the seeds with both recessive characters visible. This

yellow-round   parents   green-wrinkled

gametes

F₁

gametes →
| ＼ male
female ＼

gametes of F₁

	Y R Y R	Y r Y R	y R Y R	y r Y R
	Y R Y r	Y r Y r	y R Y r	y r Y r
	Y R y R	Y r y R	y R y R	y r y R
	Y R y r	Y r y r	y R y r	y r y r

F₂

From Plant Life *by Wilson and Haber*
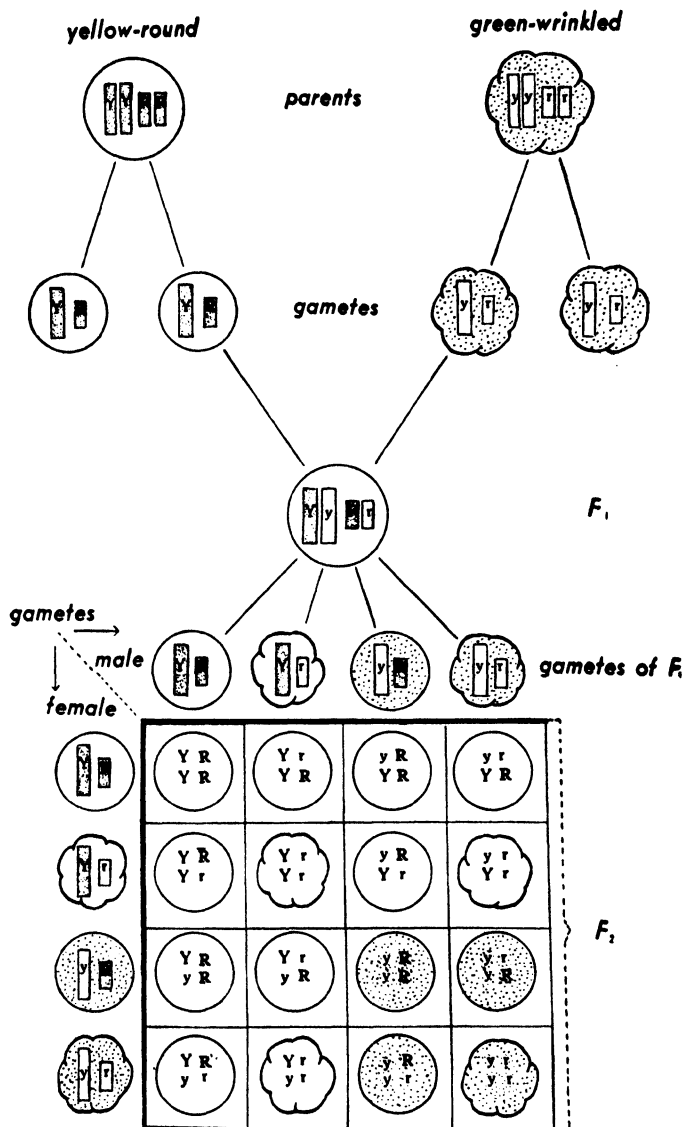
Fig. 186. Dihybrids. The results of a Mendelian inheritance when yellow-round peas (YR) are crossed with green-wrinkled peas (yr). The behavior of the respective genes is indicated within the peas. Circles represent roundness; scalloped edge, wrinkledness; clear seeds, yellow; stippled seeds, green.

9 : 3 : 3 : 1 ratio is a phenotypic ratio, for not all of the yellow-round, yellow-wrinkled, or green-round seeds are homozygous, as is shown by the fact that the yellow-rounds, green-rounds, etc. do not all breed true. In this experiment, there are 4 kinds of organisms on the basis of their phenotypes, and 9 kinds on the basis of their genotypes. The lack of correspondence between these numbers can be explained on the same basis, as in the case of the 3 : 1 appearance and the 1 : 2 : 1 genetic-constitution ratios in the F_2 generations of monohybrid crosses in the case of complete dominance. According to the law of independent assortment, the characters which come together in one generation as the result of a cross behave independently and can combine in various ways to form offspring quite unlike the parents of the F_1 generation. This law is illustrated by many crosses between organisms differing in two characters (**dihybrid crosses**); for example, independent assortment occurs in crosses between homozygous white-disc and yellow-sphere squashes, which produce in the F_2 generation about 9 white-disc to 3 yellow-disc, 3 white-sphere, and 1 yellow-sphere squashes.

There are many characters in living organisms which do not exhibit independent assortment, but which remain together and are transmitted together from one generation to another, instead of behaving independently. This phenomenon is known as **linkage**, and characters of this type are said to be linked. Linkage is explained by the occurrence of a number of hereditary determiners (**genes**) upon the same chromosome; when a particular chromosome is transmitted from a parent to an offspring, all of the genes on that chromosome ordinarily remain together and thus the characters which they control are inherited together. The phenomenon of linkage constitutes an important exception to Mendel's law of independent assortment. Quite accidentally Mendel investigated characters, the genes of which are located on separate chromosomes; thus, in Mendel's peas, when chromosomes were transmitted from parents to offspring, the genes for the characters which Mendel studied were carried on these separate chromosomes independently and were inherited independently by the offspring.

The three Mendelian laws of inheritance described above are the general principles which govern many hereditary phenomena, other than mutations, in living organisms. There are some characters which do not behave in strict accordance with these principles (e.g., those characters involved in incomplete dominance, linkage, etc.) but generally the generalizations which Mendel derived from his work on peas apply to most of the hereditary phenomena in living organisms.

3. THE MECHANISM OF INHERITANCE

Every organism, both plant and animal, which develops as a result of sexual reproduction begins its existence as a single cell, termed a **zygote,** which is the product of fusion of a male gamete (sperm) with a female gamete (egg). All that parents contribute to an offspring, then, are sex cells, and all of the hereditary traits which parents transmit to their offspring are carried in these gametes, which thus constitute the only organic connection from generation to generation. Since these gametes are the only living connections between parents and progeny, they must carry all of the hereditary potentialities of the offspring. The fundamental structural and behavior characters of an organism are thus mapped out for its entire life at the time when the zygote from which it develops is formed. As stated earlier in the chapter, the expression of these hereditary features is frequently modified by environmental conditions, but the fundamental nature of the hereditary equipment is normally not altered by external factors, at least not in the life-span of an individual. Well-fed mice are larger and healthier than starved mice, but both bear the characteristic features of mice. Certain kinds of peonies, as well as other plants, frequently do not produce their best blossoms until several years have passed after they are planted; they bear the hereditary determiners for characteristic kinds of flowers, but the visible expression of the determiners does not occur until the plants have made and stored sufficient food to make possible the production of the desired flowers. In this case, the hereditary potentialities are present but their appearance is influenced by the physiological conditions of the organism.

Thus, the relation between heredity and environmental effects is clearly stated: the fundamental *qualitative* features of organisms are determined by heredity, the *quantitative* expression of these features in most cases is influenced by physiological conditions and by factors of the external environment. An organism inherits from its parents *po-tentialities;* the development of these potentialities is conditioned largely by the mode of life and the experiences of the individual.

There is preponderant evidence that the chromosomes (review the section on mitosis in Chapter VI) of cells are the carriers of most hereditary determiners. The number of chromosomes is constant for the body cells of each species of living organism. Not only is the number of chromosomes in a species constant, but the forms and identities of chromosomes are constant through the nuclear divisions

in the cells of the species. This constancy of numbers and of identity, correlated with the constancy of hereditary traits in the members of a given species, is important evidence in favor of the chromosome theory of inheritance. Additional support is received from various types of experimental work which have shown that the alteration or removal of chromosomes or parts of chromosomes from cells produces changes in the hereditary characters of offspring from cells thus treated.

In recent years, the treatment of various plants with *colchicine*, an alkaloid, has been found to induce marked changes in the chromosomes of treated plants, usually increasing the numbers of chromosomes. Correlated with these altered chromosome numbers are changes in various characters of the treated plants, additional evidence that the chromosomes are intimately concerned with hereditary phenomena.

The hereditary determiners, or genes, are borne on chromosomes, apparently in linear fashion. Each gene seems to involve a single trait; sometimes several genes may influence the expression of one trait. When a chromosome divides in the process of mitosis, each of the genes is divided and when the two new chromosomes formed by this splitting separate, they carry identical, corresponding genes. In every body cell of all living organisms which originate from a process of sexual reproduction, there are two sets of chromosomes, one set a descendant of chromosomes which came from the male parent, the other set a descendant of a group of chromosomes which came from the female parent. These maternal and paternal chromosomes are paired; that is, for every maternal chromosome there is a corresponding paternal chromosome, similar in structure, size, and the nature of its genes. The members of such a pair of chromosomes are said to be **homologous.** The number of chromosomes in an organism arising from sexual reproduction is termed the **diploid** number, and is the sum of the maternal and paternal chromosomes. For example, the body-cells of onions contain 16 chromosomes, 8 of which are paternal, 8 maternal in origin. In some organisms there is in each cell a pair of chromosomes which are not homologous, or in the case of uneven chromosome numbers there is one extra chromosome without a homolog. These extra or non-homologous chromosomes usually are concerned with the control of sex and are called **sex chromosomes.**

The behavior of chromosomes in the formation of gametes prior to reproduction is of fundamental importance in explaining the phenomena of heredity. During the stages which lead to gamete formation, the diploid number of chromosomes is always reduced to one half.
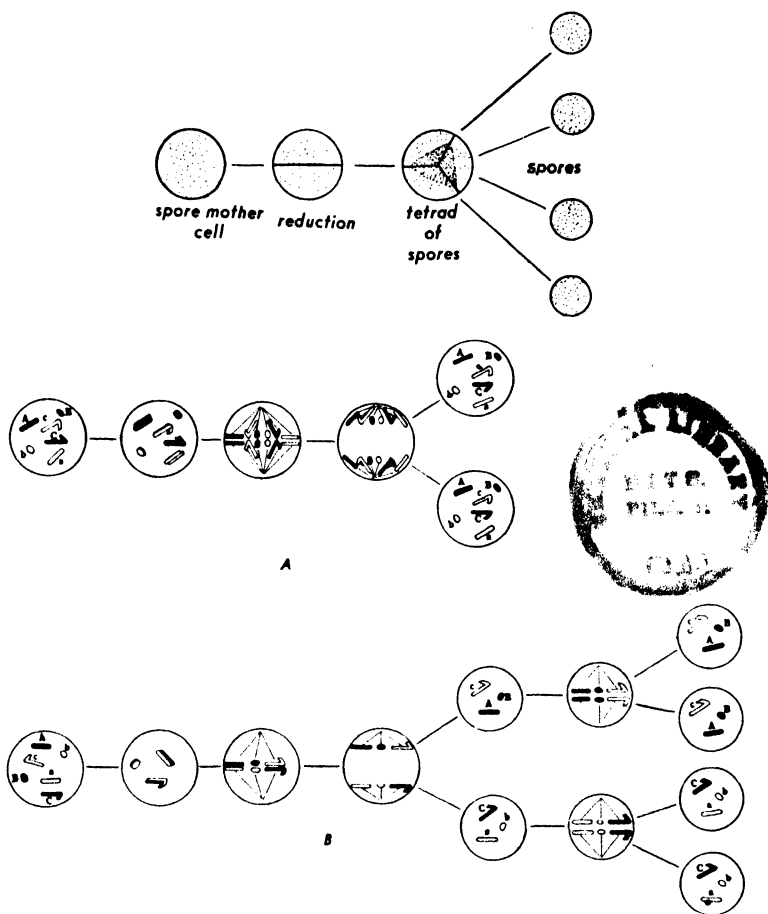
Fig. 187. Diagram to show spores formed from a spore-mother cell.
Diagrams comparing the behavior of the chromosomes in mitosis with their behavior
in reduction division. A. Diagram of mitosis. B. Diagram of reduction division.

In all plants above the Thallophytes and in many Thallophytes as
well, reduction division occurs in a diploid cell known as a **spore-
mother cell.** During the first division of a spore-mother cell, the ho-
mologous chromosomes separate from each other, one group moving
toward one pole of the spindle, the other group moving toward the
other pole of the spindle. Usually following the separation of the ho-
mologous chromosomes, a cell wall is formed across the spore-mother
cell separating the two groups of homologous chromosomes. As a result

of this *separation* of the members of each pair of homologous chromo-
somes and the formation of a cell wall, two haploid (monoploid) cells
are formed. While the homologous chromosomes are separating, they
also begin to split longitudinally, each homologous chromosome usually
showing a distinct longitudinal split during the first division. Following
the formation of the two haploid cells from a spore-mother cell, the
chromosomes in the two cells undergo a mitotic division, in which each
chromosome completes its splitting into two chromosomes, which
then separate. Cell-wall formation occurs again, as a result of which
there are four haploid cells produced from a spore-mother cell as a
result of two divisions, the first of which, the reductional or **meiotic**
division, involves the separation of homologous chromosomes and the
formation of two haploid cells, the second division resulting in a
splitting of the chromosomes in the two haploid cells and producing
from them four haploid cells. This complicated series of events is
represented in Figure 187. In most plants, each of these four haploid
cells formed from a spore-mother cell does not become a gamete but
grows into a phase which later produces gametes, or sex cells.

In flowers, there are two kinds of diploid spore-mother cells, one
kind formed in the anthers, the other kind in the ovules. Each spore-
mother cell in an anther forms four haploid spores (pollen grains)
which grow into pollen tubes within which the haploid gametes are
formed. A spore-mother cell in an ovule similarly forms four haploid
spores within the ovule; three of these disintegrate. The fourth grows
into the haploid embryo sac, which contains the haploid egg. When,
in fertilization, a sperm fuses with an egg, the diploid chromosome
number is restored; this number persists through the embryo and
through the plant into which it grows, until the plant reaches maturity
and forms its spores from spore-mother cells, preparatory to the de-
velopment of gametes. Each gamete then contains one set instead of
two sets of chromosomes. When the separation of homologous chro-
mosomes at reduction division occurs, the direction in which either
member of a pair of homologous chromosomes moves is a matter of
chance. As a result, each of the cells arising from reduction division
has a different set of paternal and maternal chromosomes; however,
only one member of each pair of homologous chromosomes is present
in each cell. Both members of such a pair do not pass into the same
daughter cell.

When fertilization occurs, the diploid number of chromosomes, is
restored, following the fusion of a male and a female gamete, during

which their respective haploid chromosome sets come together in the zygote. This union of maternal and paternal chromosomes in fertilization and their later separation by reduction division in the formation of gametes, according to chance, explains why fertilization causes new combinations of ancestral traits, why different determiners occur in the various gametes of a hybrid, and why both parents in reproduction transmit hereditary characters. When a homozygous individual forms gametes, these are all of the same type, because the homologous chromosomes which are separated in reduction divisions are alike in that they carry identical genes. In the production of gametes by a heterozygous organism, however, the chromosomes which separate at reduction division do not all bear similar genes, for they have been contributed to the heterozygous individual by different types of parents. Thus, the gametes produced by heterozygous organisms are of *different* kinds with respect to various traits which they carry, not of the same kind as in homozygous organisms. As the result of the varying unions of the different kinds of gametes formed by hybrids (heterozygous plants or animals), different characters are brought together and thus different types of offspring are produced.

Figures 187 and 183 represent the behavior of genes in meiosis and in fertilization. In such genetic diagrams, each gene is usually represented by a single letter. Since body-cells contain paired genes on homologous chromosomes, two letters are used to indicate these paired genes in a parent. In the events which lead to gamete formation by a parent, the number of genes in the gametes is reduced — that is, both members of a gene pair are no longer together, having separated in meiosis. Thus, to indicate the fact that gametes contain only one gene of each gamete pair, single letters are used to represent these genes. To indicate the paired genes for tallness in a homozygous tall parent, the letters TT are usually used; when such a parent forms gametes, the haploid gene number of the gametes is indicated by a single T. Capital letters are ordinarily used to represent dominant genes, small letters to represent recessive genes. Thus, TT would indicate that a parent was a homozygous dominant tall parent, tt would designate a homozygous dwarf parent, and Tt would represent the heterozygous condition of the offspring of a cross between them. In homozygous parents, for example TT and tt, all gametes are alike with respect to the particular gene in question. In a heterozygous parent, such as Tt, two kinds of gametes are produced, one kind bearing the T gene, the other kind the t gene.

4. PLANT BREEDING

The discovery of the fundamental laws of plant breeding had two results: it stimulated the scientific investigation of heredity in all kinds of organisms, and led to the practical application of the knowledge derived from such investigation to the breeding of new and better types of economically important plants and animals.

As stated earlier in the chapter, new varieties of plants occasionally arise by mutation, that is, by sudden, unpredictable changes in the hereditary determiners of an organism and a concomitant change in structure or behavior. Mutations are heritable; they are passed on from generation to generation. The rate at which mutations are produced in certain organisms can be artificially increased under experimental conditions, for example, as a result of X-ray treatment, but mutations thus induced have not been of desirable or useful types. Thus, man is unable to control mutations or to produce them at will. He is able to make use of them and to propagate them once they have developed, but the conditions which induce their origin have been till now beyond his control, except in the experimental instances mentioned above.

The chief methods by which man can actively produce or isolate new kinds of plants and animals are **hybridization** and **selection**.

Selection is a very old method of improving the quality of domesticated organisms. It is based upon the fact that organisms of the same species or variety vary among themselves, and tend to pass on to their offspring many of these variations. It is a matter of common knowledge, for example, that certain families of human beings rank unusually high in intelligence and that the members of successive generations of these families generally possess superior mental ability. In other families, low-intelligence prevails and is a common feature of its members through many generations. Some plants are more resistant to diseases than others of the same species and their offspring sometimes inherit in part at least the greater resistance of their parents. Some plants are taller. or yield better crops than other plants of the same species and often pass these more desirable features on to their progeny. From a large group of plants of the same variety or species, the individuals which possess the desired qualities in greatest degree are selected. Their seeds are kept and planted, and from the plants into which they grow, the best individuals again are selected. Their seeds are planted and selections again made from the plants which their

seeds produce. This selection process is often continued through many generations until a superior type of plant, with respect to a single character or group of characters, is isolated. **Mass selection** involves. choices from groups of individuals; **line selection** is the selection of an individual plant and the development of a new line of plants from its progeny. The latter method usually results in greater uniformity in the progeny of the selected plants than does mass selection.

Among the qualities in plants which are improved by selection are fruit yield, flower color and size, hardiness, and resistance to disease. Selection has developed many famous and valuable types of plants, such as Reid's Yellow Dent corn, Leaming corn, certain sugar-beet varieties, Red Fife wheat, various oat and tobacco varieties, etc.

In some kinds of plants, the practice of selection entails difficulties. In many cases, selected varieties gradually revert back to less desirable ancestral forms and thus the process of selection must be carried on constantly to assure a continuance of superior varieties. Further, the rate of progress in selection toward a desired type is often very slow, so that long periods of time are required in some plants to achieve the wanted improvements.

The other principal method of breeding organisms is hybridization or cross-breeding. In this method two varieties or species are crossed, and their progeny in the F_1 and F_2 generations are carefully watched and tested for superior new combinations of hereditary characters. The chief value in hybridization lies in the fact that it produces new combinations of characters. When a new desirable hybrid combination is secured, it may be perpetuated by vegetative reproduction, that is, by means of cuttings, graftings, etc. Hybrids can be reproduced without change only by vegetative methods; when they are propagated by seeds, assortment of genes occurs and their offspring are thus of different types. It is for this reason that the seeds of many kinds of horticultural plants, such as certain apple varieties, Burbank's Royal walnut, and others, do not "come true" — that is, they do not grow into plants of the same, desirable variety. Only by vegetative reproduction can hybrid varieties be maintained as constant types without further change. Another value in hybridization is the fact that hybrids are frequently more vigorous and give better yields than their parent varieties, a phenomenon termed **hybrid vigor.**

Only organisms which are very closely related can be hybridized. Hybridization is practiced most commonly between varieties of the same species; less frequently, hybridization is successful between very

closely related species. In a few cases, hybrids between related genera (a genus is a group of closely related species) have been produced.

SUMMARY

1. The tendency of progeny to resemble their parents is termed heredity. The science of heredity is genetics.

2. All multicellular organisms differ in some slight degree from their parents; this tendency is called variation.

3. Variations in living organisms are of three common types:

    a. Modifications induced by environmental changes. These are not inherited.

    b. Mutations. These are sudden, distinct changes which result from alterations in the hereditary determiners (genes) within an organism. Mutations are heritable.

    c. Combinations. These are heritable changes brought about in offspring as a result of the sexual reproduction of parents which differ in some degree. Offspring which are produced by parents of differing varieties or species are called hybrids.

4. The fundamental laws of heredity were enunciated by an Austrian monk, Gregor Mendel, in 1866.

5. Mendel's laws may be stated as follows:

    a. The law of dominance: when two contrasting characters from differing parents are brought together in an offspring, one of the characters (the dominant character) may mask ~~or hide~~ the other character (the recessive character).

    b. The law of segregation: in the offspring of hybrid plants, a segregation or separation of contrasting characters occurs.

    c. The law of independent assortment: the various characters which come together in a hybrid generation as the result of a cross behave independently and can combine in various ways when the hybrid generation forms its offspring.

6. A monohybrid (single character) cross is one between plants which differ in only one character. A dihybrid (two character) cross is one between parents which differ in two characters.

7. The first generation resulting from a cross between differing parents is termed the first filial (F_1) generation; the offspring of the F_1 generation are termed the second filial (F_2) generation.

8. A homozygous plant is one which has come from parents of the same type and which breeds true; that is, its offspring are similar to each generation and to the parent. A heterozygous (hybrid) plant is

an offspring of different types of parents and does not breed true; that is, its offspring are not all like each other or like the parents, but some of them resemble more distant ancestors.

9. The term genotype means the genetic constitution of an organism. The term phenotype refers to the external appearance of an organism. Because of the phenomenon of dominance, the phenotype does not always indicate the genotype of an organism.

10. Some exceptions to Mendel's laws have been discovered by more recent investigators. Among these exceptions are the following:

a. Incomplete dominance. In the contrasting characters of many species of plants, both characters are equally expressed, neither being dominant over the other.

b. Linkage. Not all characters are inherited independently of other characters, but some characters remain together from generation to generation, a phenomenon termed linkage. Linkage is explained by the occurrence of a number of hereditary determiners (genes) upon the same chromosome.

11. Most of the characters of organisms are controlled by genes, which seem to be in linear arrangement upon chromosomes. When a chromosome divides in mitosis, the chromosomes and their genes split longitudinally, so that each chromosome with its genes is duplicated and each daughter cell receives duplicate chromosomes.

12. In the body cells of organisms which result from sexual reproduction, there are two sets of chromosomes. One set is contributed by the male sex cell (sperm), the other by the female sex cell (egg). In these two sets, the chromosomes (and their genes) are paired; that is, for each kind of chromosome, there is usually another of the same type.

13. When such an organism is about to reproduce, it forms directly or indirectly sex cells which have half the number of chromosomes of the body cells. The double (diploid) chromosome number is reduced to the single (haploid) chromosome number of the sex cells by a process known as meiosis. During meiosis, the segregation of genes and thus of the characters which they determine occurs.

14. When sexual reproduction occurs, the haploid chromosome set of one sex cell combines with the haploid chromosome set of another sex cell and the diploid chromosome number is thus restored in the zygote. When two differing types of gametes fuse, the different genes which they bear are brought together and thus different types of offspring are produced.

15. The development of new and improved types of plants is largely a result of crossing related plants and choosing the hybrid offspring with desirable combinations of characters from the parent plants.

These hybrids may then be maintained in most cases by vegetative propagation.

16. New types of plants may also be introduced by propagating individuals which have developed improved characters as a result of mutation.

17. Improved types of plants may also be developed by selection of individuals with desirable variations and by breeding them continuously with themselves or with other individuals with similar desirable variations.

18. Only organisms which are closely related can be hybridized.

PART III

The Plant Kingdom

The Classification of Plants; Reproduction and Alternation of Generations

1. THE CLASSIFICATION OF PLANTS

THE WISH to classify objects is a basic trait of the human intelligence. We constantly classify the things and happenings about us with respect to their effect upon our physical or mental lives. This wish to classify is expressed in the branch of botany known as **taxonomy,** which is concerned primarily with the classification of plants. The plant world is composed of nearly 335,000 kinds (species) of plants, which we classify into groups of varying size and relationship. Botanists and laymen alike classify plants, the former principally to satisfy their intellectual urge toward neat, orderly, and meaningful arrangement, the latter chiefly to distinguish among plants which are beautiful, ugly, weedy, poisonous, edible, etc.

Botanists differ in their opinions concerning the classification of plants. These differences of viewpoint are attributable to the fact that our knowledge concerning true relationships among certain kinds of plants is fragmentary and that therefore the classification of such organisms is in part a matter of subjective opinion rather than of objective, scientific fact. Since opinions covering these doubtful relationships among different kinds of plants vary, the systems of classification which botanists contrive differ correspondingly. The fact that such systems vary should not lead to discouragement, but rather to stimulation to further scientific investigation in an effort to clarify disputed points concerning relationships among plants.

Botanists endeavor to classify plants in a manner to indicate wherever possible the actual relationships among the plants which are being classified. Such a **natural system** is the ultimate goal of taxonomic research. An **artificial system** of classification is one which is based upon convenience, rather than upon actual relationships. Artificial

systems are often employed to classify organisms whose kind and degree of relationship are not known; these are likewise used for convenience and simplicity in grouping organisms for purposes of identification. A common artificial classification of plants is one which separates all plants into herbs, trees, and shrubs, for the sake of speed in identification. Obviously such an arrangement is not natural, for totally unrelated plants often have similar growth-habits and external forms. Apple trees are much more closely related to strawberries than they are to elm trees, yet, in an artificial system of classification of the type mentioned in the preceding sentence, elms are placed closer to apples than are strawberries.

The classification of various groups of living organisms may be based upon a number of criteria — size, color, manner of obtaining or making food, anatomy, external form, methods of reproduction, etc. The criteria considered to be most significant for purposes of classification are structural features of vegetative parts, especially with reference to vascular anatomy, the nature of reproductive processes, and the structure of reproductive parts. Reproductive criteria seem most significant as bases of classification because they are less susceptible to the molding effects of changing environmental conditions. The sizes of leaves, lengths of stems, amount of root growth, color, and other features vary widely with external factors, but the structure of flowers, fruits, and seeds is relatively constant under such conditions. Certain structural features of vascular tissues of vegetative parts of plants are frequently used to supplement reproductive criteria in the classification of plants. In a number of cases, totally unrelated species of plants have almost identical gross, external structure; certain members of the cactus, milkweed, and spurge families, growing in arid and semi-arid regions, have barrel-shaped stems, heavy cutin layers, spines, and other morphological similarities, but differ widely in the structure of their flowers and fruits. If they were classified according to the gross structure of their vegetative parts, they would be considered as closely related, but differences in their flower structure indicate that their relationship is actually very distant.

Botanical classification involves the subdividing of the different kinds of plants into groups of varying size and nature. Just as a continent is divided into nations, nations into states or provinces, states into counties, counties into towns and townships, towns into blocks, etc., so the plant kingdom is separated into a number of categories of varying magnitude and quality.

The basic classificational unit in plant (and animal) taxonomy is the **species**. A species may be defined simply as a single **kind** of living organism — for example, a soft maple is a species, red clover is a species, the coconut palm is a species, etc. Biologists usually consider species as the smallest units in the classification system which are structurally similar, have common ancestors, and maintain their characteristic features *in nature* through innumerable generations. White oaks always have certain characteristic features of white oaks, soft maples of soft maples, etc. Sometimes different types of organisms occur within a species; for example, all domesticated dogs belong to one species, yet there are many kinds of dogs — collies, fox terriers, Airedales, etc. All of them have the specific characteristics of dogs, yet they vary. These individual types, however, *will not maintain their differences in nature*. If dogs of all kinds are left to their own devices, their progeny in a number of years will have been reduced to a canine common denominator; all of the differences among collies, poodles, etc., will have vanished and a single type of dog will be the result. Such kinds of organisms within a species are termed **varieties**; they persist usually only when they are prevented by man's interference from breeding with other varieties. In nature, they would breed with other varieties and thus produce eventually a common type.

A group of closely related species is called a **genus** (plural **genera**). For example, all kinds of roses taken together constitute the rose genus. The individual rose varieties and species differ among themselves in minor ways, but they all possess a common quality (which we might call "roseness") which stamps them as very closely related kinds of plants. Another example of a genus is the pine genus, composed of many species of pines — white pines, sugar pines, slash pines, longleaf pines, etc. — which vary among themselves but which all possess a fundamental quality of "pineness."

A group of closely related genera is called a **family**. For example, the rose family is composed of many genera, among which are the rose genus, the apple genus, the strawberry genus, the peach genus, etc. All of these genera have certain basic similarities in their floral structure but differ among each other in rather well-marked ways. The scientific names of families end in "ae"; thus the technical name of the rose family is **Rosaceae**, of the pine family **Pinaceae**, etc.

A group of related families constitutes an **order**, the scientific name of which ends in "ales." Thus the rose order (**Rosales**) is composed of the rose family (**Rosaceae**), the legume family (**Leguminosae**), the

Photo by Missouri Botanical Garden

Fig. 188. Linnaeus. The bust is in the Missouri Botanical Garden.

gooseberry family (**Grossulariaceae**), etc., all of which have certain common features of floral structure which indicates a close relationship among them.

Orders are grouped into **classes**, and classes together constitute a **division**. The plant kingdom is made up of four divisions, described briefly in Chapter III: **Thallophyta, Bryophyta, Pteridophyta,** and **Spermatophyta.**

Botanists ordinarily refer to plants by scientific names, which are derived principally from Latin and Greek words. The advantage of scientific names over common, popular names is that the former are governed in part by rules established by International Congresses of botanists and are thus uniformly regulated, and since they are based usually upon only two languages they are the same in all parts of the world. The disadvantage of common names is their great variability, not only in different countries, but even within the same country or state. For example, a common member of the mallow family is known within the Mississippi Valley by several popular names — velvet-leaf, button-weed, Indian mallow, and butter-print; its scientific name, *Abutilon theophrasti*, is the same throughout the world and is immediately recognized by botanists of all nationalities, many of whom would not know it by its many common names. Thus, scientific names constitute an international language among biologists. Scientific names sometimes commemorate people (e.g., *Forsythia*); sometimes they are derived from mythology (e.g., *Mercurialis*); occasionally they are descriptive (e.g., *alba*-white, *rubra*-red, *saccharinum*-sweet, etc.), and sometimes they are

derived from words of great antiquity and unknown meaning. Scientific names may also refer to habitats (e.g., *Ranunculus aquaticus*, or water buttercup) and geographical locations (*Rhus canadensis*).

A scientific name consists of two words, the first (capitalized) the name of the genus, the second the name of the species. For example, the scientific names of some of our common oaks are *Quercus* (genus name) *alba* (species name), *Quercus rubra* (red oak), *Quercus macrocarpa* (bur oak), *Quercus velutina* (black oak), etc. Among the roses are *Rosa setigera* (climbing prairie rose), *Rosa rubiginosa* (sweet brier), *Rosa cinnamomea* (cinnamon rose), etc. This system of using two words as the scientific name of an organism is termed the **binomial system** and is commonly used by both botanists and zoologists in the naming of plants and animals. The binomial system was first used extensively by Carolus Linnaeus (1707–1778), a great Swedish botanist (Figure 188).

Following the scientific name of every organism is an initial or abbreviation, which indicates the name of the scientist who first described and named the particular species. For example, *Zea mays* L. (corn) was named by Linnaeus, as were also *Pisum sativum* L. (pea), *Solanum tuberosum* L. (potato), and many others. *Rosa virginiana* Mill. was named and first described by Philip Miller, *Rosa setigera* Michx. by André Michaux, and *Wisteria macrostachya* Nutt. by Thomas Nuttall.

The most common classification of the divisions and classes of the plant kingdom is the following [1]:

> *Division I — Thallophyta*
>   Subdivision 1 — Algae
>   Subdivision 2 — Fungi
> *Division II — Bryophyta*
>   Class 1 — Hepaticae (Liverworts)
>   Class 2 — Musci (Mosses)
> *Division III — Pteridophyta*
>   Class 1 — Filicineae (Ferns)
>   Class 2 — Equisetineae (Horse tails)
>   Class 3 — Lycopodineae (Club mosses)

[1] This classification is a very simple one, which is in part natural, in part artificial. A recent, natural system of classification of plants, embodying present opinions concerning the relationships of the major plant groups, is presented in the appendix for interested students. The author believes that an adequate understanding of this newer classification presupposes more botanical background than the average freshman is likely to develop in an elementary botany course and that it is too complex for such students to grasp effectively. Therefore, the older and somewhat simpler system is used in this book as a pedagogical concession, although admittedly it does not express the most recent views concerning plant relationships.

Division IV — Spermatophyta
Subdivision 1 — Gymnospermae
Subdivision 2 — Angiospermae
Class 1 — Monocotyledonae
Class 2 — Dicotyledonae

The structure, reproduction, habitats, geographical distribution, and economic significance of these various groups will be discussed in succeeding chapters.

2. REPRODUCTION IN PLANTS

Since the chief criteria of classification are based upon reproductive structures and processes, an understanding of the fundamental features of reproduction is prerequisite to a study of plant classification.

Reproduction is a process whereby organisms produce offspring and thus maintain their species. There are many variations among the reproductive activities of different kinds of plants. These varying reproductive methods are usually separated into two types: **asexual reproduction**, and **sexual reproduction**.

In asexual reproduction, no production of gametes or processes of fertilization are involved. A portion of a plant body separates from a parent body and grows, if it finds favorable environmental conditions, into a complete new individual. Among the common types of asexual reproduction in plants are **fission, budding, fragmentation, spore-formation**, and **vegetative reproduction**. Fission is the method of reproduction in many primitive plants; it is merely the division of a single-celled organism into two new single-celled organisms. Budding is a method of asexual reproduction in which a small protuberance forms on the surface of a one-celled organism. This protuberance grows until it is almost as large as the cell of which it is a part. A wall is then formed between this "bud" and the original cell, and the two cells separate. Budding is the common method of reproduction in yeasts. Fragmentation is the breaking into segments of a multicellular plant body. Each part is then able to grow into a complete new plant. Spores are specialized structures, usually one-celled, occasionally two to several-celled, which are produced by many kinds of plants; a spore separates from the parent which produced it and is able by repeated cell divisions to grow into a complete, new individual. In some water plants (algae and fungi) the spores possess protoplasmic appendages (**cilia, or flagella**) which move in undulating fashion and

propel the spores through the water. Such motile spores are called **zoospores.** A structure which produces spores is called a sporangium. Reproduction by means of runners (stolons), cuttings, grafting, leaves, tubers, etc., are examples of vegetative reproductive methods.

Sexual reproduction involves the fusion of **gametes,** or sex cells, in pairs. The cell produced by the fusion of two gametes is called a **zygote.** In a few primitive plants, the gametes are all alike in structure and in size, though they may differ somewhat in their physiology. Such gametes are termed **isogametes,** and the process of reproduction with which they are concerned is termed **isogamy.** The more common and more advanced type of sexual reproduction, termed **heterogamy,** involves gametes which are unlike in size and structure, as well as in certain of their physiological activities. These **heterogametes** are termed **eggs** (female gametes) and **sperms** (male gametes). Eggs are larger than sperms and are most frequently non-motile; sperms are often equipped with cilia or flagella and are in such cases able to swim actively in a liquid medium. The fusion of an egg and a sperm in the embryo sac of an angiosperm is an example of heterogamous sexual reproduction.

As described in the preceding chapter, a reduction in chromosomes from the diploid to the haploid number occurs at some time prior to the formation of gametes. When sexual reproduction occurs, the diploid number of chromosomes is restored as the result of the fusion of haploid gametes in pairs.

In some plants, certain algae, for example, the zoospores and isogametes are almost indistinguishable in structure, differing only in size. Because of this fact, it is believed by many botanists that sexual reproduction may have originated from asexual reproduction, possibly as a result of the fusion of diminutive zoospores.

3. ALTERNATION OF GENERATIONS

A conspicuous feature of reproduction in most plants, with the exception of some of the thallophytes, is a phenomenon termed **alternation of generations.** This phenomenon merely means that the complete life history, or life-cycle, of a plant is made up of two phases, or generations, one of which is an asexual generation, reproducing by spores (the **sporophyte**), the other a sexual generation, reproducing by gametes (the **gametophyte**). In the reproduction of gametophytes, eggs and sperms are formed, an egg fusing with a sperm to produce a zygote.

This zygote does not grow into another gamete-bearing plant, but grows into a plant which reproduces asexually by spores (the sporophyte). Similarly, these spores do not produce more spore-bearing plants, but grow into gamete-forming plants (gametophytes).

A zygote, which bears the diploid chromosome number, grows into a sporophyte plant, or generation, which likewise has the diploid chromosome number in all its cells. When the sporophyte generation forms spores, reduction division (meiosis) occurs, as a result of which the spores are haploid — that is, they contain the single or reduced chromosome number. The gametophyte generation, into which a spore grows, contains the haploid chromosome number in all of its cells, including the gametes which it forms. When the gametes fuse in the process of fertilization, their haploid chromosomes are brought together in the zygote and thus the diploid number of chromosomes is re-established. This number persists through the sporophyte, which the zygote forms, until reduction division brings about the haploid number in the spores.

In some thallophytes, there is a definite alternation of haploid, gamete-forming plants and diploid, spore-forming plants. In others, reduction division occurs when the zygote begins to divide. The diploid phase in such plants is limited to the zygote, all other parts of the plant being haploid.

In all bryophytes, pteridophytes and spermatophytes, alternation of generations occurs. In bryophytes, the gametophyte, or sexual generation, is larger and more complex structurally than the sporophyte generation; further, it is green and therefore autotrophic, whereas the less conspicuous sporophyte generation is partially or wholly dependent upon the gametophyte for its nourishment. In pteridophytes, the sporophyte generation is autotrophic and is the larger, more complex, and more conspicuous generation, the gametophyte being only a fraction of an inch in diameter, though green and autotrophic. In the spermatophytes, as in the pteridophytes, the sporophyte generation is the more complex and larger generation. However, the gametophyte generation, instead of being green and autotrophic as in pteridophytes, lacks chlorophyll and is therefore dependent upon the sporophyte, within the tissues of which it develops, for its nourishment.

In all the divisions of plants, the gametophyte generation lacks differentiated vascular tissues, whereas in the sporophyte generation, vascular and strengthening tissues are usually well-developed. This fundamental difference in body architecture has apparently been

the chief factor which has made possible the growth of the sporophytes
of the higher plant groups into very large plants and which has limited
gametophytes generally to rather small size.

As stated above, alternation of generations occurs in all of the three
higher divisions of the plant kingdom and in some of the thallophytes
as well. The structural features of the alternating generations vary in
the different divisions of plants, as will be described in succeeding
chapters.

SUMMARY

1. There are approximately 335,000 species of plants known at
present. Many more species will be found as botanists continue their
exploration of the earth's surface.

2. Natural systems of classification attempt to classify plants in ac-
cordance with their relationships. Artificial systems of classification are
used chiefly for convenience and for the classification of plants whose
actual relationships are unknown. A natural system of classification
is the goal of taxonomy.

3. The principal criteria used in classifying plants are structure and
reproductive methods.

4. The basic classificational unit is the species. A group of closely
related species is a genus, a group of genera is a family, a collection
of related families constitutes an order, and orders are grouped into
classes. Classes together constitute a division.

5. The members of the plant kingdom are ordinarily separated into
four divisions:
    a. Thallophyta.
    b. Bryophyta.
    c. Pteridophyta.
    d. Spermatophyta.

6. Scientific names constitute an international language of science
and are based principally upon Greek and Latin words.

7. A scientific name consists usually of two words: the first is the
name of the genus and is usually capitalized, the second is the name
of the species and is usually not capitalized. The practice of applying
a two-word scientific name to a plant or animal is termed the binomial
system.

8. Following each scientific name is an initial or abbreviation in-
dicating the name of the man who first described and named the
plant or animal species in question.

9. The various methods of reproduction in plants may be separated into two groups: asexual and sexual. Sexual reproduction involves the fusion in pairs of gametes or sex cells. Asexual reproduction is any method of reproduction which does not involve gametic fusion.

10. Isogamy is a type of sexual reproduction which involves the fusion of structurally similar gametes. Heterogamy is a sexual process which involves the fusion of structurally dissimilar gametes.

11. A male gamete is called a sperm, a female gamete, an egg.

12. Among the common methods of asexual reproduction are fission, budding, fragmentation, spore-formation, etc.

13. Alternation of generations is a phenomenon in which the complete life-cycle of a plant consists of two phases or generations: a gametophyte (sexual) generation which reproduces by means of gametic fusion, and a sporophyte (asexual) generation which reproduces by spores. Each generation in turn gives rise to the other — hence the term "alternation of generations."

14. Alternation of generations occurs in some Thallophyta and in all members of the three higher divisions.

15. The gametophyte generation possesses the haploid (single) chromosome number, the sporophyte generation the diploid (double) chromosome number.

16. The gametophyte generation in all plants lacks differentiated vascular tissues, whereas the sporophyte generation, at least in Pteridophyta and Spermatophyta, has vascular tissues and thus has been able to reach a much larger size than the gametophyte generation.

Thallophytes: Algae

THE THALLOPHYTES are structurally the simplest kinds of plants, forming the lowest of the divisions of the plant kingdom. They vary in size from microscopic, one-celled organisms to multicellular plants reaching several hundred feet in length. There is less cellular differentiation in thallophytes than there is in other kinds of plants. Such tissues as xylem, phloem, endodermal layers, etc., are absent from the bodies of thallophytes; except in a few brown algae which have somewhat specialized conducting cells resembling sieve tubes. The term **thallus** is applied to such a plant body with relatively little differentiation of tissues. In some thallophytes, such as seaweeds, there often occur structures which in form resemble the roots, stems, and leaves of higher plants. Such structures in thallophytes are usually not referred to by these names, for they lack the characteristic tissue differentiation of these organs of higher plants. The sex organs of the thallophytes are often one-celled, in contrast to the many-celled sex organs which occur in higher divisions of plants. Thus, the thallophytes are relatively simple structurally as compared with angiosperms, gymnosperms, and other more highly developed kinds of plants.

Several types of reproduction occur in thallophytes. Asexual reproduction is very common; spore-formation, fragmentation, budding, and fission occur in the various kinds of thallophytes. Both isogamous and heterogamous sexual reproduction occur among the members of this division.

It is generally believed by biologists that some of the living thallophytes are similar to the first types of organisms which appeared on the surface of the earth. Evidence in support of this belief is derived from the facts that they are very simple in structure, that they are commonly aquatic plants (the first living organisms were doubtless water plants), and that several thallophytes have been found as fossils in very old rock strata. Among these, there are fossils believed to be more than one

billion years old, similar to present-day blue-green algae. These are among the oldest fossils of plants still found living on the earth.

The thallophytes are divided into two groups: **algae** and **fungi,** of which there are approximately 18,000 and 90,000 species respectively. The chief difference between algae and fungi is a physiological one; the algae possess chlorophyll and therefore manufacture their own food, whereas the fungi lack chlorophyll and thus must ordinarily get their food parasitically or saprophytically. In many features of morphology and reproductive behavior, certain algae and fungi are very similar; botanists generally regard them as parallel groups which differ primarily in their manner of nutrition. The physiological distinction between algae and fungi is thus to be regarded as primarily an artificial one, since on the basis of similarities in structure and reproductive methods, certain algae resemble certain fungi more than they do other algae and are probably more closely related to them.

The algae are chiefly water plants. Most of the members of this group live in oceans, rivers, ponds, ditches, swimming pools, etc. A few species do not live in water but grow on stones, fence posts, and the bark of trees, chiefly in moist locations which are shaded from direct sunlight. As a rule, the species which inhabit fresh water do not grow in salt water, and vice versa. There is great variation in size, structure, and reproductive methods among the various kinds of algae; the only features common to all algae is their possession of chlorophyll, and their usually aquatic nature. The algae constitute a very heterogeneous group of organisms, many of which are doubtless only distantly related. As such, they should probably be segregated into groups more nearly based upon their actual relationships (see Appendix), but in this text, for the sake of convenience and ease of study, these relationships will not be described in detail.

The classification of algae is based upon reproductive features and upon the morphology of the various members of the group; in some cases there is a correlation between these structural and reproductive features, and the color of algae. The names of these colors are commonly used to refer to these particular groups. Students should remember, however, that the actual separation of these algae is based upon their structural and reproductive characters, and that the coincidence of color with these qualities is secondary.

A commonly-used, simplified classification of the algae separates these plants into the six following groups: **flagellates, blue-green algae, green algae, brown algae, red algae,** and **diatoms.**

1. BLUE-GREEN ALGAE (MYXOPHYCEAE)

These are morphologically the simplest of all algae, and are often considered among the most primitive kinds of plants (Figure 189). Many of them are one-celled, others are colonial forms, in which one-celled individuals remain together in **filaments** (thread-like growths) or sheets or balls. The cells of colonial blue-green algae are usually held together in a mass of mucilaginous slime which is secreted by the algal cells. Their cells contain no organized nuclei, though chromatin

GLEOCAPSA

NOSTOC

OSCILLATORIA

ANABOENA

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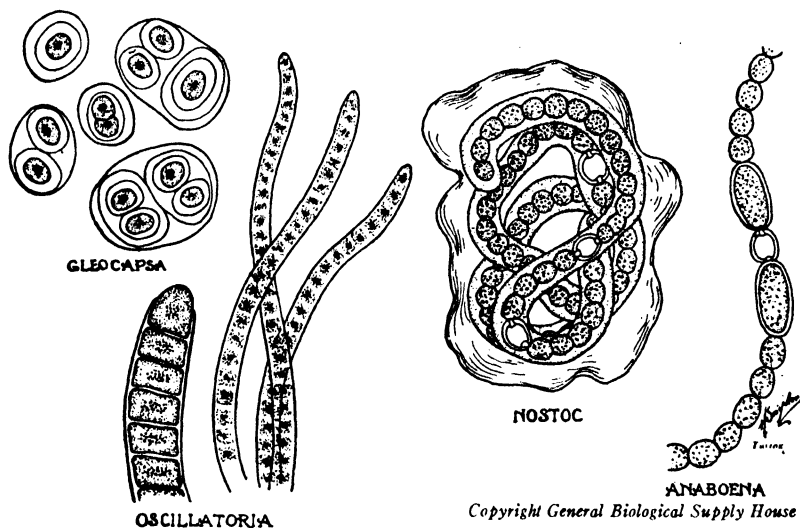
Fig. 189. Common blue-green algae.

granules are scattered in their cytoplasm, and there are no plastids present. Their color is due to the presence of a bluish pigment along with the chlorophyll which is dispersed in the cytoplasm. Reproduction in the blue-green algae is entirely asexual, by fission. In addition, certain blue-green algae under unfavorable environmental conditions may form resting spores. A common genus of blue-green algae is *Oscillatoria*, so called because its filaments exhibit slow oscillating movements in water.

The blue-green algae occur in both fresh and salt water (more commonly the former) and as bluish-green, sometimes almost black, slimy growths on the surface of wet soil, rocks, etc. A few species of blue-green algae are very tolerant of high temperatures and thrive in the vicinity of hot springs in Yellowstone Park and similar regions. These algae

deposit carbonates in the form of rock known as **travertine.** They are important in nature and to man because their growth and decay add organic materials to soils and thus increase their fertility, they are sources of food for certain organisms of the water and soil, and they frequently contaminate water-supplies, producing in them a slimy material and often foul tastes and odors. It has been reported that live-stock have died as a result of drinking water in which many blue-green algae were growing. Blue-green algae have been reported to occur in human intestinal tracts, apparently without benefit or harm.

2. FLAGELLATES

These are one-celled organisms which swim about in the water in which they live by means of the movements of cilia or flagella (Figure 190). They vary in shape; some are spherical, some ovoid, some pear-shaped. Each one-celled individual contains a single nucleus and usually one or more chloroplasts. Some are green, others yellowish-green or brown in color. Those flagellates which lack chlorophyll are usually classified among the protozoa of the animal kingdom, as are frequently the chlorophyllous species as well. Some of the non-green flagellates are classified by some botanists as members of the fungi. In many flagellates there is a tiny, usually red **eyespot,** which is sensitive to light and apparently acts as a primitive type of eye. Reproduction in the flagellates is commonly asexual, by means of simple cell division. Frequently one-celled flagellates remain together in colonies.

One of the most interesting and significant features of the flagellates is the fact that many of them possess both plant and animal features. Many are chlorophyllous, a typical plant characteristic, but many of them in addition are able to ingest solid food, a typical animal characteristic. Thus, these organisms are classed by botanists and zoologists respectively as algae and as protozoa. This mixture of plant and animal characteristics is of evolutionary significance, for it supplies evidence in support of the belief that some of the first living organisms to appear on the earth were neither plants nor animals but possessed certain features of both and that the higher types of plants and animals may have evolved from some such intermediate ancestral types. Many biologists believe that the green flagellates are the ancestral forms of other kinds of plants, with the green algae possibly their nearest relatives, and that the non-green flagellates are perhaps the original ancestors of the animal kingdom.

The flagellates occur commonly in fresh water and in salt water. They are found in lakes, ponds, ditches, and often in swimming pools and other rather quiet bodies of water, as well as very commonly in the oceans of the world. Some of them form pink or red patches, called "red snow," on snow and ice in arctic regions. The flagellates are important sources of food for fish, crustaceans, and other animals of fresh and salt water. They constitute a portion of the diet of blue whales, the mouths of which contain straining devices for collecting these minute organisms and other microscopic algae in large quantities from sea water. One of the commonest genera, *Euglena*, occurs generally in ponds, aquaria, swimming pools, etc. It causes water to become greenish and turbid and often odoriferous, and for this reason is regarded by sanitary engineers as undesirable in water to be used for bathing and drinking. If a piece of cotton is tied over the mouth of a hydrant and the water is allowed to drip slowly through the cotton for two or three days, the cotton may show greenish stains after this time, as a result of the filtering out of flagellates and other microscopic algae from the water.
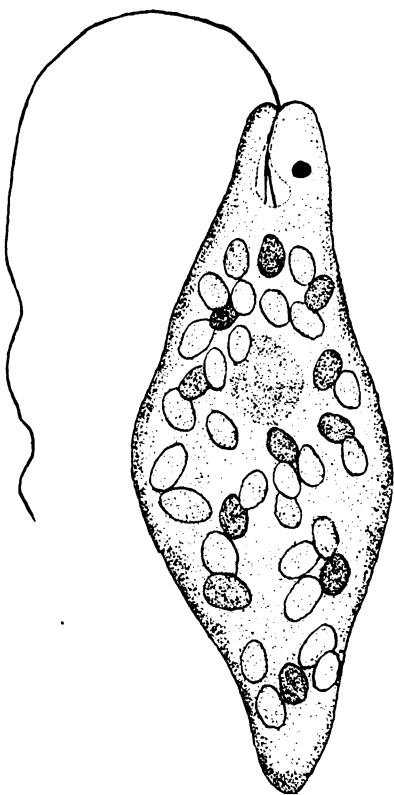
Fig. 190. *Euglena*, a flagellate, showing flagellum, eyespot, and chloroplasts.

3. GREEN ALGAE (CHLOROPHYCEAE)

These are chiefly fresh-water algae which are usually grass-green in color. Some species live in the ocean, some on trees, moist rocks, soil, etc. Some species are one-celled, others are colonial, and many of them are multicellular, having the form of branched or unbranched filaments or less frequently, flat sheets of tissue. The cells of green algae contain chloroplasts and organized nuclei.

Reproduction in green algae is by a variety of methods. Asexual reproduction is achieved by zoospores, cell division, and fragmentation. Sexual reproduction occurs in most species, some of which are isogamous, others heterogamous.

Among the common genera of green algae are *Protococcus*, *Ulothrix*, *Spirogyra*, and *Oedogonium*. The plants of *Protococcus* are unicellular and grow most frequently on damp rocks, tree-trunks, fences, walls, etc.,
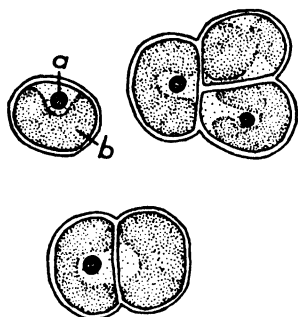
Fig. 191. *Protococcus*
a. nucleus. b. chloroplast.
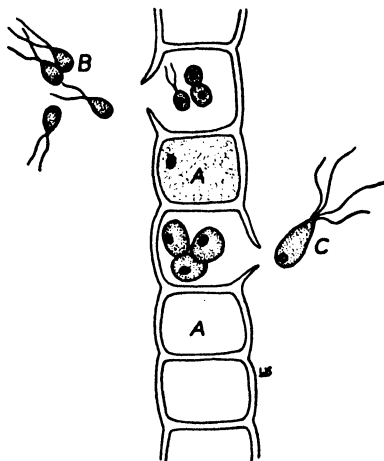
Fig. 192. Portion of *Ulothrix* filament
A. Cells of filament.
B. Isogametes.
C. Zoospores.

in diffuse light. Each *Protococcus* plant (Figure 191) contains a nucleus and a single large chloroplast in its protoplasm, and reproduces by cell division, its only method of multiplication. Following reproduction these spherical, one-celled plants frequently remain together in colonies of varying size.

Ulothrix (Figure 192) is a genus of filamentous algae which are usually attached to sticks or pebbles in the water in which they grow. The basal cell of each filament is ordinarily modified into a specialized **holdfast** which anchors the filament to its solid substratum. Each cell of *Ulothrix* contains a chloroplast and a nucleus. Under certain conditions, the protoplasm in certain cells of the filaments divides to form green ciliated **zoospores**, from 2 to 16 or, rarely, more per cell. When a zoosporangium is mature, an opening appears in its wall and the zoospores are liberated into the water, in which they swim about by means of their cilia. Each zoospore is green and has an eyespot like that of a flagellate. After several hours or days of movement, these spores become attached to solid objects in the water, following which

the cilia are lost and the single-celled spores grow by cell division into new filaments. *Ulothrix* reproduces sexually by means of isogametes. These are produced in the same manner as zoospores, which they resemble in structure and color except that they are much smaller. These iso-gametes swim about in the water after their liberation. When a gamete comes in contact with a gamete produced by a cell of another filament, sexual fusion oc-curs and a zygote is formed. The zygote, after a brief period of activity, usually remains in a resting condition for some weeks, then begins to grow if external conditions are favorable, each zygote producing 4 to 16 zoospores, which swim about in the water, become attached, and then grow into new filaments.

The reproduction of *Ulothrix* is con-sidered important from an evolutionary standpoint. The zoospores (asexual) and gametes (sexual) are almost identical in structure, differing mainly in size. It is believed that sexual reproduction may have developed in primitive plants by the fusion in pairs of zoospores which were so small that they contained too little food to enable them to grow sep-arately into new filaments. *Ulothrix* might be interpreted as representing such a phenomenon. Also, the zoospores of *Ulothrix*, since they resemble very strikingly certain flagellates, are re-garded by some botanists as evidence in support of the theory that some of the green algae evolved from flagellate ancestors.

Fig. 193. *Oedogonium*
A. Cells of filament.
B. Oogonium with egg.
C. Antheridium with sperms.
D. Sperm.
E. Fertilization pore.

Oedogonium (Figure 193) is another common filamentous, fresh-water genus of green algae, which resembles *Ulothrix* in many ways. Some of its members are free-floating filaments, others are attached by hold-fasts to solid objects in water. *Oedogonium* reproduces asexually by frag-mentation and also by large, ciliated zoospores, which are produced

singly in certain cells (sporangia) of the filaments. Sexual reproduction also occurs in *Oedogonium* by means of heterogametes. Certain cells of a filament become **oogonia,** each producing a single egg which is retained within its oogonium, not liberated into the water, as in *Ulothrix.* Certain other cells (**antheridia**) of a filament produce sperms, two in each antheridium. The sperms escape from the antheridia and swim by means of their cilia to an oogonium as a result of their attraction by substances excreted into the water by the oogonium. The sperm enters a pore in the oogonium wall, and fertilizes the egg inside. The zygote, after a dormant period, is set free by the decay of the oogonium wall and germinates, producing four zoospores, each of which grows into a new filament. As in *Ulothrix,* the zygote of *Oedogonium* is diploid. Reduction division occurs when the zygote germinates and the zoospores of both genera and the filaments into which they grow are haploid. The sperms and eggs are likewise haploid. The heterogamous reproduction of *Oedogonium* is considered more advanced than the isogamous reproduction of *Ulothrix,* and is similar in its fundamental feature — the fusion of structurally and physiologically differentiated gametes, an egg and a sperm — to the sexual reproduction of higher types of plants. Most botanists believe that the ancestors of the land plants probably developed originally from plants similar to certain heterogamous green algae.

Spirogyra (Figure 194) is another common filamentous genus of green algae found in stagnant ponds, pools, horse troughs, aquaria, etc. It is easily recognized by the large, spiral-shaped chloroplasts in its cells. No zoospores or other types of spores are produced by *Spirogyra.* Reproduction is asexual by fragmentation and sexual by means of an isogamous process known as **conjugation** (Figure 195). In this type of reproduction, two filaments lie side by side, held together by the mucilaginous secretion around them. At their points of contact, tiny protuberances form from opposite cells of the two filaments. These protuberances come into contact at their tips and when they have reached a certain size their end walls disappear, as a result of which continuous hollow tubes connect the opposite cells of the filaments. Following the disappearance of the end walls, the entire protoplast of one cell slowly passes through the tube and fuses with the protoplasm of the opposite cell with which the first cell is connected. The zygote thus formed develops a thick wall and remains dormant for several weeks or months. As a rule all of the protoplasts of a single filament behave in the same manner; that is, all of the protoplasts of one filament

Fig. 194. A green alga, *Spirogyra*, as seen by dark-field illumination. Notice the spiral chloroplasts.

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Fig. 195. Portion of a filament of *Spirogyra*. Note the spiral chloroplasts and central nucleus. Stages in the conjunction of *Spirogyra*
A. Early stages.
B. Late stages showing zygotes, conjugation tubes, and empty cells of one filament.

remain stationary and those of the other filament move toward the stationary ones of the first filament. The process of conjugation is considered isogamous because the gametes are alike in size and in structure. That they differ physiologically is obvious because of the difference in their behavior. The migrating gamete is sometimes called a male gamete, the stationary one the female gamete. Usually conjugation occurs between the cells of different filaments, but in a few species conjugation occurs between adjacent cells of the same filament. When a zygote germinates, reduction division occurs and the new filament which the zygote produces is haploid.

In *Spirogyra* and certain other algae, the onset of sexual processes is frequently correlated with unfavorable environmental conditions. Zygotes are generally dormant and thick-walled, and are very resistant to desiccation, low temperatures, and other adverse external circumstances. When environmental factors become favorable once more for active growth, zygotes usually germinate and produce new filaments.

The green algae are important to man in a number of ways. They are common agents of water pollution in lakes, water tanks, aquaria, etc. Like some of the blue-green algae they impart undesirable fishy flavors and odors to the water in which they grow. Usually the most commonly encountered pond-scums are members of the green algae. The green algae may be considered beneficial to human life in that through their photosynthetic activity, they add oxygen to the water in which they live, thus making more of this gas available for fish and for aerobic bacteria which bring about the decomposition of organic materials in water and aid in the purification of sewage in streams. If the growth of algae becomes too dense, the oxygen content of the water may be lowered by the nocturnal respiration of the algae to such a point that fish die of suffocation. Undesired algae in ponds, swimming pools, aquaria, etc., can usually be eradicated by adding minute quantities of copper sulfate (one part of copper sulfate to from 500,000 to 20,000,000 parts of water) to the water, a quantity so small that it is without effect upon human beings or other animals who drink or live in the water. The green algae are also important as food for fish and other water organisms. Sea-lettuce (*Ulva*) is a marine, green alga which is used as human food in some parts of the world. In India, dried *Oedogonium* and *Spirogyra* are considered delicacies in the human diet. Some of the green algae secrete carbonates and thus aid in the construction of rock deposits, principally in oceanic islands.

4. BROWN ALGAE (PHAEOPHYCEAE)

These are the largest and most complex structurally of all algae. They are chiefly marine plants, occurring most commonly in the cooler waters of the world's oceans. They are all multicellular and possess a variety of forms. Some are ribbon-like, others are plate-like, filamentous, and in some cases superficially similar to higher plants in that they possess leaf-like and stem-like structures (Figures 198, 199). Their tissues are normally not highly differentiated as are the tissues of higher plants; however, in some species of brown algae, cells resembling the sieve-tubes of higher plants have been found. The brown algae are usually attached by holdfasts (Figure 200) to rocks or other solid objects beneath or at the surface of the water. They frequently bear air bladders, hollow, spherical or ovoid structures within which air is held and which aid in floating the upper portions of the thallus on or near the surface of the water (Figure 196). The brown algae possess a

Fig. 196. A large Pacific-coast kelp, *Pelago-phycus*. Note the large air bladders.

brown pigment which normally obscures the green color of the chlorophyll present in their tissues.

Many of the brown algae grow in the intertidal zones (Figure 197) along the seashore and thus undergo alternating periods of submergence and of exposure to air. Such species usually are covered with gelatinous, colloidal substances which hold water tenaciously and thus prevent desiccation of the thalli during the periods of exposure. The algae of this type are commonly called **rockweeds**. One of the common genera of rockweeds is *Fucus* (Figure 203). *Fucus* plants are flat, branched thalli, attached to rocks by means of holdfasts and buoyed up in the water by small air bladders. *Fucus* lacks asexual spores and reproduces chiefly by a heterogamous sexual method and fragmentation. At the tips of the thallus branches are swollen cavities (**conceptacles**), some of which contain antheridia, others oogonia. Each antheridium produces numerous sperms, each oogonium eight eggs. When they are mature, the eggs and sperms are liberated into the water, in which fertilization occurs. The zygote by cell division grows into a new *Fucus* plant. The thalli of *Fucus* are diploid, reduction division occurring at the time of gamete formation. The diploid number is restored by fertilization.

The largest and most complex brown algae are termed **kelps**. Some of these live for many years and reach lengths of several hundred feet. The kelps usually grow in deeper water and thus do not experience alternating submerged and exposed periods. Many of the kelps have air bladders which frequently reach lengths of five or six feet. The kelps frequently have leaf-like and stem-like portions and are the most highly differentiated of all algae (Figure 201). Many of the kelps exhibit an al-

Fig. 197: Rockweed (*Fucus*) growing on intertidal rocks. California coast.

Fig. 198. A Pacific-coast brown alga, *Macrocystis*. Note the air bladders.

Fig. 199. Seaweed washed up on shore of California. (The plant with the air bladders is a species of *Macrocystis*.)

ternation of well-marked hap-
loid gametophyte and diploid
sporophyte generations.

The brown algae are of all
algae doubtless the most im-
portant directly to man. Some
of them yield iodine, absorbed
from sea water, in commer-
cially-obtainable   quantities.
Many of them contain con-
siderable quantities of min-
erals, particularly potassium
(potash). These algae are fre-
quently removed from beaches,
dried, burned, and their ashes
used as fertilizers for soils and
as ingredients for soap manu-
facture. Some of them are used
directly as fertilizers without
being burned. The use of kelps
for fertilizers is especially com-
mon in the Orient, in Eastern
Canada, Alaska, New Eng-

Fig. 200. A brown alga (*Egregia*), showing
holdfast attached to rock.

land, France, and South America. Some of the brown algae are im-
portant sources of food for fish and other water animals, and, when
they have been removed from the ocean, for cattle. Many brown algae
serve as food for human beings, particularly in the Orient, where they
are eaten fresh or after they have been dried. Algae are sometimes
baked or made into soups and broths which are then eaten. Some 30
species of marine algae are commonly eaten by Japanese and Chinese.
The Japanese sink bamboo poles into shallow water; spores of various
kinds of algae become attached to these poles and grow into mature
plants which are then harvested. Algae are not highly nutritious foods,
but they do supply some carbohydrates, as well as vitamins, minerals,
and gelatinous substances with laxative action. One of the food uses of
brown algae is as imitation candied citron, or sea-weed candy. Some
brown algae are used in medicines as sources of iodine and other min-
erals. One of the most recently announced uses for brown algae is the
manufacture of rayon (artificial silk) through a process devised by a
British chemist.

Fig. 201. A large seaweed on the coast of Washington.

5. RED ALGAE (RHODOPHYCEAE)

The red algae, like the brown, are almost entirely salt-water plants, living usually in the warmer waters of the ocean. They are able to grow at greater depths than are the brown algae. The red algae possess a red pigment which usually masks the color of the chlorophyll present in their plastids. The bodies of red algae are multicellular and are rather complex structurally, though they are not so highly differentiated as are the browns. They are much smaller than most brown algae, rarely exceeding a foot in length. Some of the red algae are filamentous, others are ribbon-like, plate-like, or much branched, resembling feathers or delicate fern leaves. The red algae reproduce asexually by spores and by heterogamous sexual processes.

The red algae are important sources of food for fish and other animals of the seas, and they frequently serve as sources of food in the

Fig. 202. Holdfasts of a seaweed (*Macrocystis*). California coast.

human diet. The Irish moss and sea kale of the Atlantic Coast of North America are red algae which are eaten by human beings, especially in New England. Irish moss and its products are used in curing leather, in shoe polish, shaving creams, cosmetics, and shampoos. In Europe and the Orient, the use of red algae as food plants is considerably more extensive than it is in the United States. Many of the red algae yield mucilaginous materials employed in the manufacture of glue and lubricating jellies, and a gelatinous material, known as agar-agar, which has a number of important uses. Agar absorbs large quantities of water and "sets" when cool to a gelatin-like consistency. It forms the chief material for the preparation of artificial growth-media for bacteria and is thus tremendously important in bacteriological work; it is used as a thickening material for soups and broths, and is employed to give "body" to ice-creams, puddings, certain pastries, and canned fish. Agar is also used as a mild laxative in medicinal preparations, as a sizing material for textiles, and in the clarification of liquors. The red algae, like the brown algae, contain considerable quantities of minerals in their tissues and for this reason are harvested from the sea along with brown algae for use as a fertilizer for cultivated soils.

Many of the red algae secrete carbonates and thus aid in the building of coral reefs. Algal formations of this kind have been found in rock strata more than a hundred million years old. Many of the large coral reefs in the Indian Ocean, in the region of the Dutch East Indies, and in the waters surrounding Australia have been built up largely through the lime-secreting activities.
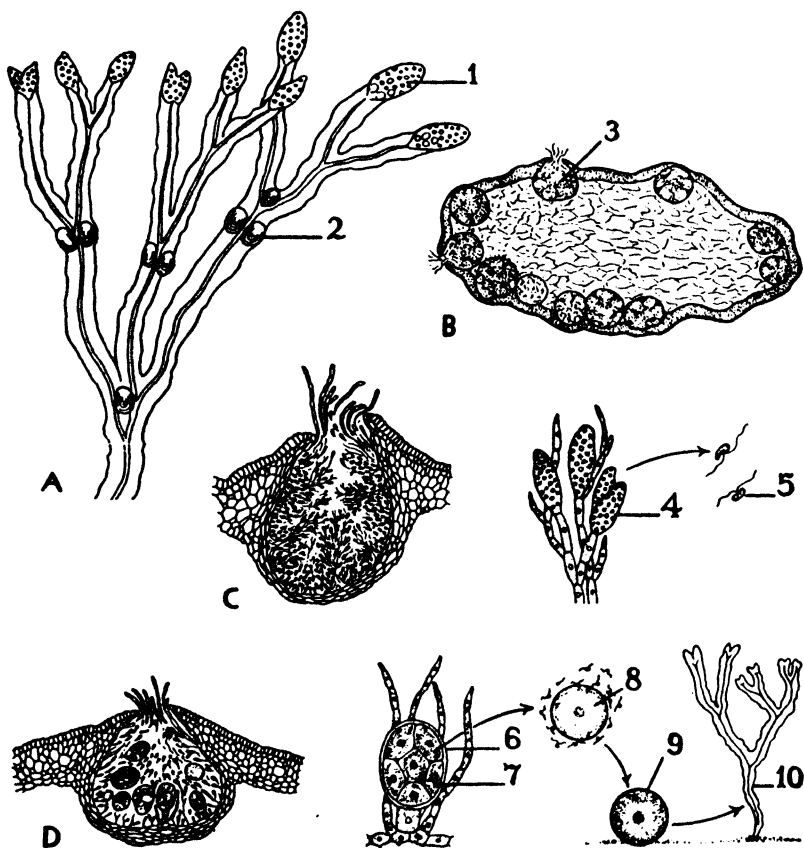
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Fig. 203. Fucus

A. Portion of thallus.
B. Cross-section of fruiting tip with an-
   theridial conceptacles.

C. Antheridial conceptacle.
D. Oogonial conceptacle.

1. Fruiting tip, with conceptacles.
2. Air bladder.
3. Antheridial conceptacle.
4. Antheridium.
5. Sperm cell.
6. Oogonium.

7. Egg cell (eight produced in oogoni-
   um).
8. Liberated egg cell, surrounded by
   sperm cells.
9. Fertilized egg.
10. New thallus produced.

6. DIATOMS (DIATOMEAE)

These are algae of rather uncertain relationship which are one-celled and which have curious, beautifully sculptured walls which are impregnated with silica and which consist of two halves that fit together like the bottom and lid of a small box (Figures 204, 205). They are widely distributed in the sea, in lakes and ponds, and in soil. Diatoms are for the most part chlorophyllous and thus make their own food. They reproduce by cell division and also by a simple sexual process.

Diatoms occur in enormous numbers in the fresh and salt waters of the world. They frequently make ocean waters turbid and discolor ocean currents for hundreds of miles. Over one hundred thousand diatoms may often be found in a quart of sea water, and a cubic yard of turbid, muddy river water may contain over 8,000,000 of them. They occur rather abundantly even in purified drinking water and may be found therein by microscopic examination. Fortunately, they are harmless and give no sign of their presence as they pass through human digestive canals.

The diatoms are important to man in a number of ways. Dead diatoms in the oceans and lakes have sunk through many centuries to ocean beds and have formed large deposits of **diatomaceous earth,** which is rich in the silica shells of dead diatoms. Some of these beds, which occur in many places on the earth, are almost 3000 feet thick. Diatomaceous earth is used extensively in the filtering and clarifying of certain kinds of liquids such as oils and syrups, in the manufacture of insulating materials for steam pipes and refrigerators, in the preparation of metal polishes, in the making of light-weight bricks, and as absorbent material in the manufacture and packing of dynamite. Diatoms are also used in the manufacture of bacteriological filters which are employed by bacteriologists, physicians, and other scientific workers in removing bacteria from liquids. If a liquid which contains some disease-producing qualities is passed through a diatomaceous, bacteriological filter and still retains its ability to produce disease, it is assumed to contain filterable viruses, which are able to pass through these filters. The diatoms of past ages have contributed extensively to the formation of petroleum and thus are of great significance to us at the present time. Living diatoms are among the most abundant microscopic organisms (**plankton**) of the oceans and, with the flagellates, are an important source of food for fish and other animals of the sea. Very intricate nutritional relationships exist among the myriad organisms

Fig. 204. *Pinnularia nobilis,* a diatom. 430x.
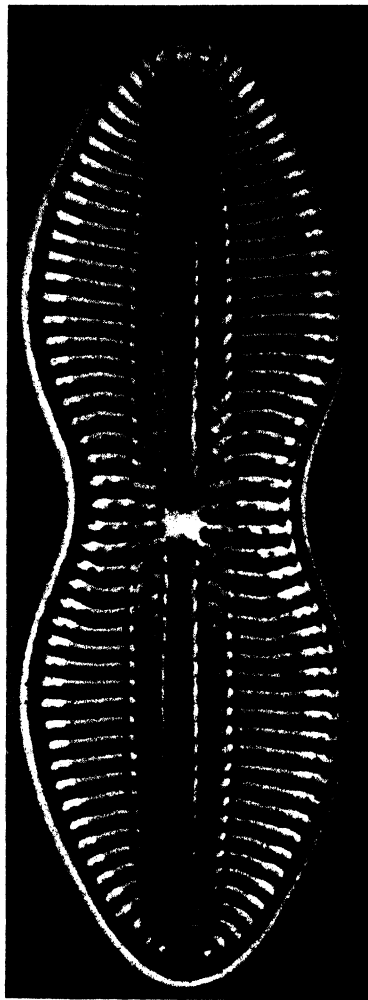
Fig. 205. *Navicula crabo,* a diatom. 1100x.

of the sea, relationships which are indicated in the term "the food chain of the sea." The first link in this chain is the unicellular diatoms and flagellates. These are consumed by small fish, crustacea, and other small animals. These in turn are eaten by larger fish and crustaceans, these by still larger fish, etc. At the top of the food chain are such animals as the walrus, seals, and polar bears. One author has pointed out that the Eskimos live indirectly upon diatoms and flagellates, for Eskimos derive most of their food, clothing, fuel, bone tools, etc., from seals, walrus, polar bears, and whales, which either directly or indirectly through a long series of smaller organisms derived most of their nourishment from the microscopic algae of the sea. As stated earlier in the chapter, blue whales derive most of their food directly from microscopic algae, particularly diatoms. The stomachs of mature blue whales, which commonly grow to lengths of 70–75 feet and weights of 60 tons, have been found to contain as much as two tons of plankton, chiefly diatoms, at one time.

7. SUMMARY OF ALGAE

1. The algae are the oldest and simplest green plants and are structurally adapted to life in water or in moist land habitats. They are thallus plants, lacking true roots, stems, and leaves.

2. The blue-green algae are the least complex structurally of all algae. Brown algae and red algae are most complex structurally.

3. The algae are a heterogeneous assemblage of plants, the relationships of which are incompletely known.

4. In the algae are found unicellular, colonial, and multicellular organisms.

5. In the lower algae, reproduction is entirely asexual. In intermediate species, isogamous sexual reproduction and asexual reproduction occur. In the more advanced algae, reproduction is chiefly by heterogamy.

6. It seems that isogamous sexual reproduction may have originated as a result of the fusion of asexual spores of insufficient size to develop individually into new plants. Several similarities between zoospores and isogametes in such algae as *Ulothrix* furnish evidence in support of this belief. Heterogamy is a more advanced type of sexual reproduction which possibly developed from isogamy as a result of the structural differentiation of gametes into eggs and sperms.

7. Alternation of generations does not occur in all classes of algae, but is well-established in some of them, particularly in the red and brown

algae. In many species the sporophyte generation is limited to a zygote, while in others there is a definite alternation between sporophyte and gametophyte plants.

8. The brown and red algae are regarded as specialized groups which have not in the course of evolution led to the development of higher forms of plants. The green algae are considered the most likely ancestors of land plants.

9. The sex organs of some algae are unicellular, whereas those of other species are multicellular. The male sex organs are termed **antheridia,** the female, **oogonia.**

Thallophytes: Fungi

FUNGI, LIKE algae, are thalloid plants; that is, they possess only a slight degree of cellular differentiation, and lack roots, stems, and leaves. With the exception of a few species of chemosynthetic bacteria, the fungi are dependent upon externally supplied food, since they lack chlorophyll and hence cannot carry on photosynthesis. Some of them are **parasites,** deriving their food from the tissues of other living organisms, while others are **saprophytes,** obtaining their foods from non-living organic substances. Some fungi may live either as parasites or saprophytes, according to the nature of available food supplies. As a result of their heterotrophic mode of life, they are limited to places where organic materials are available. Since they do not carry on photosynthesis, they are independent of light and can live either in light or in darkness. Some of them are water plants, others are land plants limited to moist habitats or, if they are parasites, to the living tissues of their **hosts.** Many fungi are highly specialized in their nutritional requirements; the **rusts,** which parasitize grains and many other plants, live only on a few species of hosts, whereas some saprophytic forms, such as many molds, grow on a wide variety of substrates — decaying food, old leather, dead leaves, animal excrement, etc.

Some fungi are unicellular, but most species are multicellular. The cells in multicellular fungi are arranged in filaments (**hyphae**) which grow loosely over or through the substratum or which are rather tightly packed together into structures of characteristic size and form. Fungi lack plastids, but their cells (excepting the bacteria) have nuclei.

Fungi reproduce by a variety of methods, most commonly by various spores. The fungi which inhabit water produce zoospores which are structurally similar to those of algae. Those species which are not aquatic produce spores which are blown about by the wind or which are carried by insects, birds, and other animals. Other common reproductive methods in fungi are fragmentation and fission. In some

groups, sexual reproduction does not occur, in others isogamy and heterogamy prevail.

In their morphology and in their reproductive methods, many fungi resemble quite strikingly certain of the algae. Some kinds of fungi resemble algae in these respects much more than they do other fungi. In view of these marked parallelisms the distinction between algae and fungi on the basis of their food habits is doubtless a highly artificial one, as pointed out in the preceding chapter. The origins of the fungi are not known with certainty. Some botanists believe that the fungi have developed from non-green flagellates in the same direction as the algae which are believed to have evolved from green flagellates. Some fungi seem to have evolved from algal ancestors as a result of the loss of chlorophyll and the ability to carry on photosynthesis.

The fungi, like the algae, are subdivided into a number of classes, of which the following will be considered: **bacteria, algal-fungi, sac-fungi,** and **club-fungi.** The latter three groups are frequently called "higher fungi" to distinguish them from bacteria.

1. BACTERIA (SCHIZOMYCETES)

Bacteria are the smallest and structurally simplest, not only of all fungi but of all living organisms (Figure 206). They are typically uni-cellular and rarely exceed 3.5 or 4 microns in length (a micron is about one $\frac{1}{25,000}$ of an inch). A few species of bacteria are approximately .5 micron ($\frac{1}{50,000}$ of an inch) in diameter! Of these smaller bacteria, as many as 300, placed side by side, would just cover the printed period at the end of this sentence. Bacteria are thus visible only under con-siderable magnification by high-power microscopes. There are three common forms of bacteria: spheres (**coccus** forms), rods (**bacillus** forms), and spirals (**spirillum** forms). Some of the rod and spiral forms have cilia by means of which they move through liquid media in which they are present. Other bacteria, including most of the sphere forms, lack cilia and are non-motile. A microscopic examination of bacterial cells shows that their structure is very simple. They have thin cell walls, which usually are more or less mucilaginous. There are no nuclei in bacteria; there is, however, nuclear material in the form of chromatin granules scattered through the cytoplasm. No plastids or other organized structures are present in bacterial cytoplasm.

Reproduction in bacteria is entirely asexual. A bacterial cell divides by fission into 2 new one-celled individuals. In some species of bacteria,
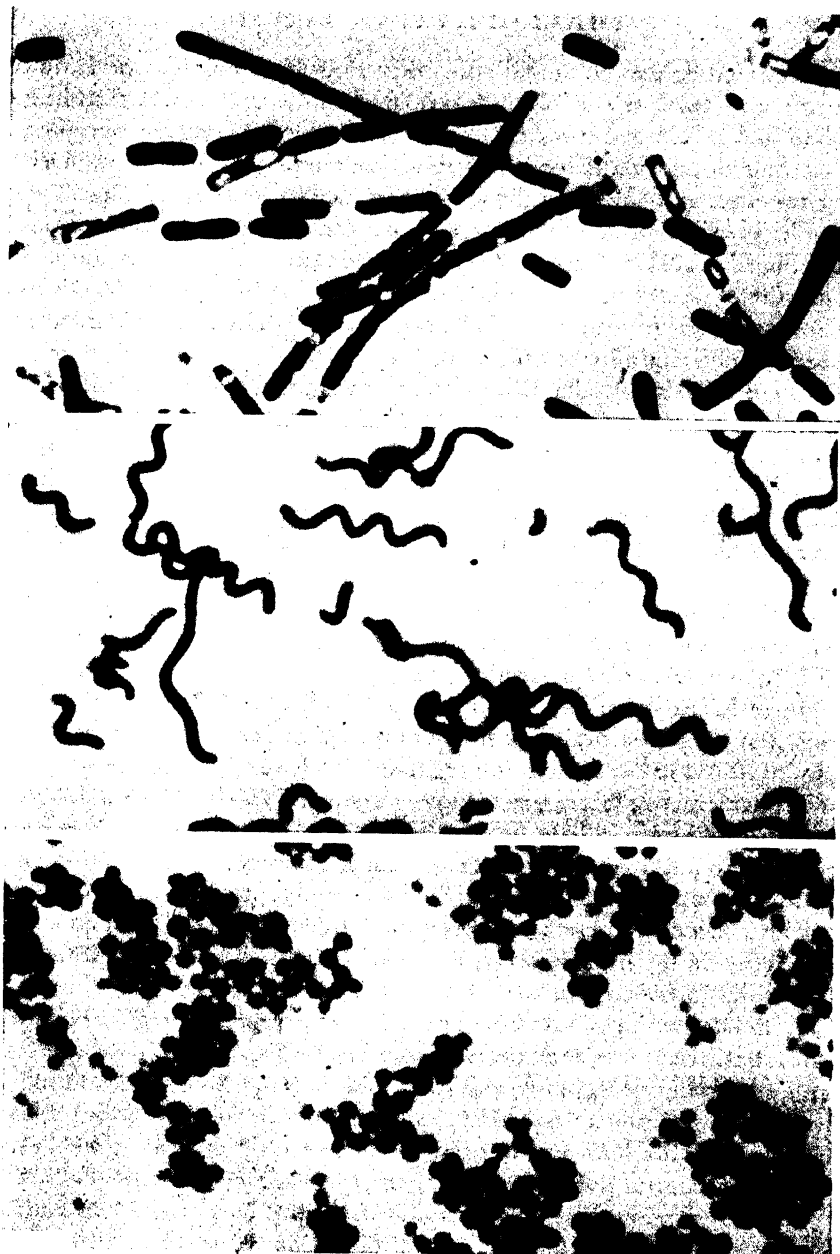
Fig. 206. *Bacillus anthrax*, the anthrax bacterium. 2300x.
Spirillum rubrum, a bacterium found commonly in water. 2150x.
Staphylococcus aureus, cause of boils and other skin infections. 2600x.

the cells, after fission, remain together and form colonies of various forms and sizes. Some of these are filamentous, others are cubical, plate-like, etc. In some bacteria, under conditions of favorable temperature and of abundant food and moisture supply, fission occurs every 20 minutes. A cholera bacterium reproducing at its most rapid rate would *in 24 hours have offspring numbering 4,700,000,000,000,000,000,000 and weighing almost 2,000 tons!* This exceedingly rapid reproduction is only theoretically possible, however, for the inadequacy of food supplies and the accumulation of toxic waste products of metabolism prevent such unlimited multiplication.

Some bacteria, under unfavorable environmental conditions, such as extremes of temperature, lack of moisture, etc., form dormant spores which can usually withstand successfully such untoward external factors. Spore production in bacteria can scarcely be considered a method of reproduction, for one bacterium forms but one spore. Thus, spore-formation does not increase the number of individuals but merely carries an individual through conditions which would probably kill a physiologically active cell. Active bacteria are usually susceptible to the destructive effects of high temperatures, of certain types of light and of ultra-violet rays, and of various chemical agents (antiseptics) and are killed upon exposure to these conditions. Thus, exposure to high temperatures and steam under pressure is a common method employed to kill bacteria in the canning of foods and in the sterilization of surgical instruments, gauze, and bandages. Carbolic acid, iodine, mercuric chloride, silver nitrate, hypochlorous acid, lye, potassium permanganate, hydrogen peroxide, formaldehyde, and many other chemical preparations are effective chemical agents which kill bacteria quickly. Some of these are so powerful that they may be used only externally on the human body, whereas others may be used as internal antiseptics in the treatment of bacterial diseases.

With the exception of some chemosynthetic species (e.g., iron and sulfur bacteria), bacteria are saprophytes or parasites. Some species are quite indifferent concerning their method of getting food and may live saprophytically at one time, parasitically at another. Many bacteria are aerobic (can live only in the presence of oxygen), others are anaerobic (cannot live in the presence of free oxygen).

Bacteria are important to man and in nature in a number of ways. Some species are harmful or wasteful, others are beneficial and useful. Among the harmful or wasteful results of bacterial activity are these:

1. Bacteria cause many serious diseases of man — e.g., tuberculosis,

pneumonia, lockjaw, typhoid fever, cholera, diphtheria, and strepto-coccus infections.

2. They cause diseases of domesticated animals — e.g., tuberculosis of cattle, hogs, etc., anthrax, chicken cholera, glanders, pneumonia, etc.

3. They cause diseases of cultivated plants — e.g., cabbage rot, fire blight of pears, citrus canker, and some of the wilt diseases (caused chiefly by the stoppage of vascular tissues by masses of bacteria) of tomatoes, potatoes, cucumbers, and squash. That bacteria can cause diseases of plants was discovered by Professor T. J. Burrill, of the University of Illinois, in 1879. The disease which he proved to be the result of bacterial infection was fire blight of pears.

4. They cause the spoilage of large quantities of human food — e.g., the souring of milk, the rotting of meat, the spoilage of wines, potatoes, fruits, etc. In their growth in such foodstuffs, bacteria frequently excrete waste products which are toxic to human beings and frequently cause severe digestive disturbances and even death.

5. Some bacteria (**denitrifying bacteria**) cause the escape of nitrogen from the soil into the air in gaseous form and thus reduce the fertility of soils.

Despite their reputation as evil-doers, bacteria actually are more beneficial to man than they are harmful. Among their valuable activities are the following:

1. Their metabolic processes are important in various industries. The manufacture of vinegar, of butter, of certain kinds of cheese, of sauerkraut, and of dill pickles, the tanning of leather, the curing of black tea and tobacco, the removal of flax fibers from the stems of flax plants, the curing of vanilla pods, and the fermentation of ensilage are examples of industrial and agricultural activities promoted by bacteria. Bacteria digest and utilize in their metabolism various sugars, starches, proteins, and numerous other kinds of organic compounds, and in their metabolic activities excrete waste products, some of which have exceedingly important industrial uses. Among these products are acetone, an ingredient used in the manufacture of explosives and other products; butyl alcohol, a widely used commercial solvent especially valuable in the manufacture of synthetic lacquers; lactic acid, of special usefulness in the tanning industry; citric acid, employed as a flavoring in "lemon" flavored confections, drinks, and other food-stuffs; vitamins, useful in medicinal preparations and foods; and numerous other organic products.

The large-scale production of such valuable materials from bacterial

metabolism is a relatively new field in the economic utilization of bacteria, and, as such, is one in which new discoveries are frequent and often very startling. For example, a species of bacterium known as *Clostridium acetobutylicum* ferments the carbohydrates in corn, molasses, and other starchy or sugary materials, and produces, as a result of its metabolic activity, acetone, methyl alcohol, and n-butyl alcohol, all three of which have important industrial uses. When this method of producing these substances was first employed on an extensive scale, acetone was the most important product. Subsequently, with the development of the modern lacquer industry, n-butyl alcohol became most important. Very recently, Vitamin B_2 has been discovered as a product of the fermentation of carbohydrates by the same species of *Clostridium*. This vitamin, which has been one of the more expensive vitamins to obtain in quantity and which is valuable as a preventative of pellagra, certain nervous disorders, and other diseases, is now another commercially important product of the fermentation of sugars and starches by *Clostridium acetobutylicum*. Careful biochemical studies of this bacterium and its nutritional peculiarities have led to the discovery that the amount of Vitamin B_2 produced by its metabolic processes can be increased about 150 times over the original quantity produced, merely by altering certain conditions in the culture of the bacterium.

2. Bacteria are significant in man's existence not only because they cause some of his most serious diseases, but they are important in that they can be used as weapons against the very diseases which they cause. Bacteria are employed in the production of the **serums** and **vaccines** which are used to develop immunity to various diseases in man. Serums are prepared from the liquid material of the blood of animals, such as horses, into which small doses of bacterial **toxins,** or poisons, are injected in increasing doses through a considerable length of time. The body of the animal forms substances, called **antibodies,** which neutralize or combat the effects of the bacterial poisons in the body. After a time, blood is withdrawn from the animal and is treated to remove the blood corpuscles and other solid matter. The clear blood liquid, or serum (known popularly as "antitoxin") contains the antibodies and is injected into the blood of a human being suffering from a disease caused by the same or a similar kind of bacteria which produced the toxins previously injected into the animal. The antibodies in the serum, if administered sufficiently early, neutralize the toxins formed by the bacteria in the person suffering from the disease and

thus make recovery possible. Serums are employed not only in the treatment of diseases already acquired, but also are used in advance as a therapeutic measure to prevent the development of diseases, such as diphtheria, to which a human being might subsequently be exposed. Serums are especially effective in treating lockjaw, diphtheria, meningitis, pneumonia, and other diseases. Occasionally the serum used for injection into a sick person is obtained from the blood of a human being who has recently recovered from the same disease and who has antibodies for that particular disease in his blood. The type of disease immunity produced by the injection of serums is sometimes termed **passive immunity.**

Vaccines are dead or weakened bacteria or other disease-producing agents or their diluted poisons which are injected directly into a person to stimulate him to build up antibodies in his body by giving him the disease in a mild form. This mild attack of disease induces his cells to form antibodies which are thenceforth able to neutralize the poisons formed by vigorous bacteria of the same type which may later enter his body. This **actively acquired immunity** is similar to that produced in an organism by a serious attack of a disease and usually persists for many years or for life. Usually one attack of infantile paralysis, cholera, typhoid, measles, and certain other diseases bring about immunity to the particular disease for life. The mild form of the disease, which is produced by the injection of dead or weakened bacteria or their much-diluted poisons, achieves the same result — the formation of antibodies which persist usually for a long time and render the organism immune to the corresponding disease. Vaccines are used in immunizing people against smallpox, typhoid fever, diphtheria, scarlet fever, cholera, bubonic plague, and certain other diseases. In some cases the bacteria which are killed or weakened for inoculation or injection into human beings are obtained in pure laboratory cultures grown on synthetic media. In other cases, as in the case of smallpox, the vaccine is obtained from calves which are suffering from cowpox. The cowpox blisters are scraped from the skin of these animals and the vaccine is prepared from these scrapings. The human patient who is inoculated with this vaccine contracts cowpox in a mild form and is thereby immunized against the very closely related smallpox for a number of years.

3. Bacteria bring about the decomposition of proteins, fats, carbohydrates, and other complex organic compounds in the bodies of plants and animals and of their waste products. Thus, they clear the earth

of organic debris and return to the soil and air the simple substances which are necessary for the maintenance of soil fertility and for the continued food-making activities of green plants. The bacterial decomposition of nitrogenous organic compounds in the absence of abundant oxygen usually results in the formation of materials of offensive odor, chiefly sulfur compounds. Such anaerobic decomposition is termed **putrefaction** or **protein fermentation.** Bacterial action is an important factor in the disintegration of sewage wastes.

The bacteria involved in the decomposition of nitrogenous organic compounds are so important in the maintenance of soil fertility that they deserve somewhat detailed description. The groups of bacteria involved in nitrogen transformations in the soil are the **ammonifying bacteria, nitrifying bacteria, nitrogen-fixing bacteria,** and **denitrifying bacteria.** Ammonifying bacteria transform various proteinaceous substances into ammonia in the soil. The ammonia thus formed usually reacts with other substances in the soil to form ammonium salts. The nitrifying bacteria of soil are of two kinds: **nitrite bacteria,** which convert ammonium nitrogen into **nitrites,** and **nitrate bacteria,** which convert nitrites into **nitrates,** the most readily utilized of all nitrogen compounds by green plants. The nitrite and nitrate bacteria are autotrophic; they obtain, by oxidizing ammonium and nitrite compounds respectively, energy which they use in the chemosynthetic manufacture of food from water and carbon dioxide. Nitrogen-fixing bacteria take nitrogen gas (which green plants cannot utilize) from the air and convert it into organic nitrogen compounds in the soil, which are subsequently decomposed by other bacteria and transformed through a series of stages into nitrates. There are two types of nitrogen-fixing bacteria: those which live in the soil and those which live in small swellings or **nodules** (Figure 207) on the roots of leguminous plants, such as clovers, alfalfa, beans, and soy-beans, and certain other species of plants. There are several kinds of nodule bacteria, each of which usually lives in the roots of a single species or variety of legume or of several closely related species. The relationship between nodule bacteria and their host plants is one of **symbiosis** (living-together), a condition of more or less mutual benefit. The bacteria secure food from the tissues of the host plant, and the host secures from the soil nitrogen which is fixed by the bacteria. It is because of this relationship that leguminous plants usually enrich the soil in which they grow, as a result of the nitrogen-fixing activities of their nodule bacteria. In order to ensure the development of nodule bacteria, pure cultures of

various strains of such bacteria are prepared commercially in laboratories and are mixed with the proper types of seeds before planting or are added to the soil in which the seeds are to be sown. Denitrifying bacteria, which are most active in poorly drained soils with large quantities of unfermented organic matter, act upon nitrates, break them down, and liberate free nitrogen gas into the air. Such bacteria are obviously undesirable, since they decrease the fertility of soils by wasting their nitrogen. The activities of denitrifying bacteria are, of course, balanced by the work of nitrogen-fixing bacteria.
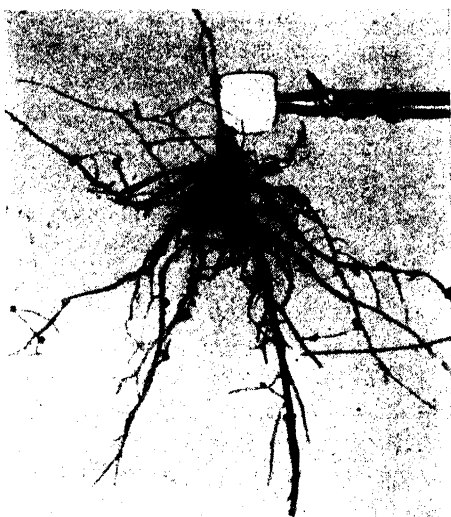
Photo by C. F. Hottes

Fig. 207. Sweet clover roots with nodules containing nitrogen-fixing bacteria.

It is believed by many botanists that there is a close relationship between bacteria and blue-green algae, for both groups of plants are similar in their complete lack of sexual reproduction, in their reproduction by fission, in the absence of nuclei from their protoplasm, and in their exclusively unicellular or colonial habits of growth.

2. ALGAL–FUNGI (PHYCOMYCETES)

The algal-, sac-, and club-fungi differ from the bacteria in that their bodies are composed of fungous threads, or **hyphae** (a mass of hyphae is known collectively as a **mycelium**). There are, however, a few species of these higher fungi which are unicellular, for example, the yeasts. The hyphae of algal-fungi lack cross-walls, a feature which distinguishes them from the hyphae of sac- and club-fungi, which have such walls. The Phycomycetes are called algal-fungi because they resemble very strikingly some of the green algae in their methods of reproduction and in certain features of their structure.

The hyphae of algal-fungi are not organized into definite bodies, but merely form cottony masses of threads upon or in their substratum. They reproduce by fragmentation, by abundantly-produced asexual
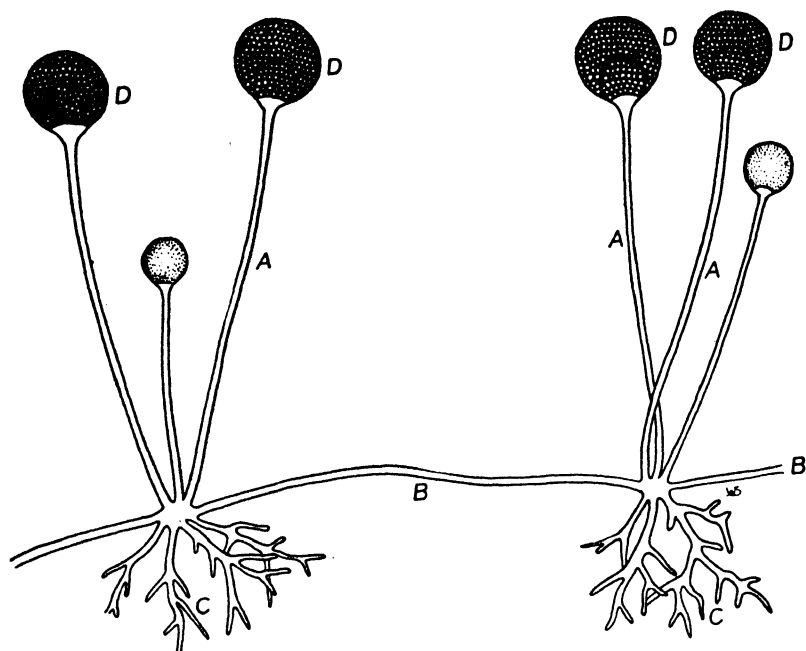
Fig. 208. *Rhizopus* (black bread mold)

A. Sporangial hyphae.   C. Rhizoids.
B. Stolons (runners).   D. Sporangia with asexual spores.

spores, and by isogamous and heterogamous sexual processes. The asexual spores are motile by cilia in the water-molds, which belong to this group. In those species which do not inhabit water, the spores lack cilia and are dispersed by wind and by insects, birds, and other kinds of animals.

Most of the algal-fungi are saprophytes and are found commonly on stale bread, jellies, decaying fruits and potatoes, dead leaves and twigs in ponds and streams, dead fish and insects, etc. One of the most ubiquitous genera of algal-fungi is *Rhizopus* (black bread mold), a white or grayish fungus which grows on bread, fruits, and other types of stale or rotting food products. The mycelium of *Rhizopus* is composed of branched, fluffy hyphae, some of which penetrate the bread or other substratum and absorb organic materials for their nourishment. Asexual spores are produced in globose sporangia at the tips of erect hyphae (Figure 208). When a sporangium is mature, its wall breaks open and the spores are liberated. They are blown by wind or fall to the substratum by gravity and, under favorable con-

ditions of moisture and food supply, grow into new hyphae. *Rhizopus* reproduces sexually (Figure 209) by an isogamous process somewhat resembling the sexual reproduction of *Spirogyra* and other green algae. Hyphae lying near each other produce lateral projections which touch at their ends. In the tip of each projection a gamete is formed. The end walls of these projections disintegrate and the two isogametes fuse, forming a thick-walled zygote, which germinates into a short hypha that produces a sporangium with asexual spores. In the sexual repro-duction of *Rhizopus*, there is a phys-iological differentiation of hyphae into strains, known as + and − strains. Sexual reproduction occurs only when hyphae of both strains are near each other; the hyphal projections which meet and form gametes are those of the two strains. This physiological differentiation of sex is similar to that in some species of *Spirogyra* in which all of the gametes of one filament move through conjugation tubes toward the stationary gametes of the other filament. In both *Rhizopus* and *Spi-rogyra* there are no morphological differences between the strains, al-though there is obviously a physiological differentiation. Thus, the sex-ual reproduction in these two genera may be considered isogamous. Other genera closely related to *Rhizopus* reproduce heterogamously.
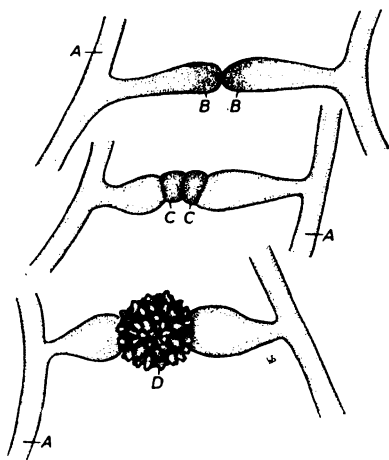
Fig. 209. Sexual reproduction of bread-mold (*Rhizopus*)

A. Hyphae. C. Gametes.
B. Progametes. D. Zygote.

Some of the algal-fungi are parasites upon other plants and upon animals. Occasionally parasitic species attack and kill fish; these species are frequently serious pests in aquaria where tropical fish are grown. Some of the diseases of higher plants are caused by algal-fungi, for example, potato late blight, white "rust" of cabbage, soft rot of sweet potatoes, and downy mildew of grapes. The potato blight fungus was responsible for the failure of the potato crop in Ireland in 1845 and the subsequent "potato famine." The downy mildew disease of grapes is an-other destructive plant malady which does tremendous damage, unless it is carefully controlled, to grapes, especially in the great vineyards of France, Spain, Italy, and other important grape-growing countries.

The saprophytic algal-fungi are important to man in that they cause extensive food spoilage and bring about the decay of organic matter, returning simpler substances to the air and soil.

3. SAC–FUNGI (ASCOMYCETES)

There are more species (about 37,000) of sac-fungi than there are of any other group of fungi. The most characteristic feature of the ascomycetes is the production, following a sexual fusion, of spores in sac-like cells termed **asci** (singular **ascus**). Each pear-shaped or ovoid ascus (Figure 210) usually contains 8 spores; less frequently only 4 spores or some multiple of 8 spores develop in an ascus. Sac-fungi are composed of numerous hyphae, which have cross-walls. In some species, such as powdery mildews,
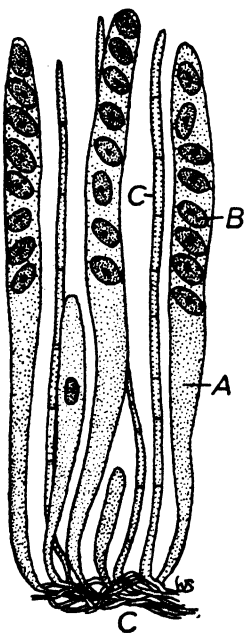
Fig. 210. Asci with spores
A. Ascus.
B. Ascospores.
C. Hyphae.
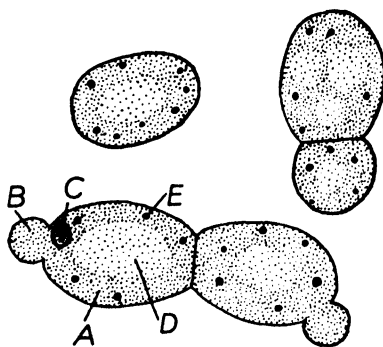
Fig. 211. Yeasts budding
A. Mature yeast cell.   C. Nucleus.
B. Bud.   D. Vacuole.
     E. Food particles.

there is no definite body, the hyphae growing in masses of irregular extent upon or in the substratum. In other species, such as morels and cup-fungi, the hyphae forming the spore-producing bodies are tightly packed into characteristic, organized structures of constant form.

Types of reproduction other than by ascospores also occur in the sac-fungi. Fragmentation, budding (in yeasts), and the formation of other types of spores are frequent. Sexual reproduction in the sac-fungi resembles somewhat that of certain red algae, a further evidence for

the belief that algae and fungi are closely related groups of plants.

Among the common groups of sac-fungi are **yeasts, powdery mildews, morels, cup-fungi, blue** and **green molds,** and others.

Yeasts are one-celled fungi which reproduce chiefly by budding (Figure 211), less frequently by ascospores. They are chiefly saprophytic, deriving their food from non-living organic matter. A few species are parasites which cause widespread skin and nail diseases, especially in the tropics. Yeasts are commercially important in the manufacture of alcohol and alcoholic beverages and in the "raising" of bread dough. The bubbles of carbon dioxide produced by the respiration of yeast plants rise through the dough, thus causing it to become light and fluffy.

Photo by C. F. Hottes

Fig. 212. *Morchella esculenta* (morel), a fleshy, edible sac-fungus.

The powdery mildews are minor parasites which form whitish or grayish patches of hyphae on the leaves of lilacs, clovers, roses, and many other kinds of plants. Though they are parasites, they usually do but little damage to their hosts. The powdery mildews produce their asci in tiny, black, spherical bodies borne on the surface of the infected leaves.

The morels, truffles, and cup-fungi (Figure 213) are fleshy ascomycetes which have definite bodies composed of tightly packed hyphae. The morels (Figure 212) and truffles are considered excellent food by connoisseurs of edible fungi.

Other important members of the sac-fungi are the blue and green molds. These, together with certain yellow and black molds are common on a variety of substrata — old leather, spoiling fruit, particularly oranges and lemons, and other materials containing organic matter. Some of these molds are responsible for the characteristic flavors and odors of certain types of cheese, for example, Roquefort and Gor-

Fig. 213. Cup-fungi (*Peziza*) on rotting wood.

gonzola; these molds are usually found as bluish-green patches in the cheese. The green color in these molds is not due to chlorophyll, but to other pigments which are in no way involved in food manufacture. Closely related to these molds are several parasites which cause ringworm and athlete's foot infections in man.

Many serious plant diseases are caused by sac-fungi. Among such maladies are peach leaf curl, Dutch elm disease, brown rot of plums, bitter rot of apples, ergot of rye, wheat, oats, and barley, chestnut blight (one of the most destructive of all plant diseases), black knot, and apple scab.

Many of the higher fungi, especially members of the ascomycetes, like certain of the bacteria, digest and ferment various organic compounds, forming as a result of their metabolic activities various substances which are important in many industrial processes. Among the products thus made are citric acid (from sugar beet pulp, artichokes, and other plant residues), lactic acid, ethyl alcohol, sterols (which are related to vitamins), a number of pigments, enzymes, particularly diastase, and a number of other important organic compounds.

4. CLUB–FUNGI (BASIDIOMYCETES)

These fungi, like the ascomycetes, are composed of hyphae with cross-walls; these hyphae form loose, irregular growths in some species, in others they are organized into definite bodies with characteristic

forms and sizes. The chief characteristic of the club-fungi is the presence of a club-like structure, or **basidium** (Figure 214), which produces, on its surface on short stalks, usually four **basidiospores**. The club-fungi also reproduce by fragmentation and other methods, but their multiplication is most commonly achieved by means of basidiospores.

The club-fungi are subdivided into a number of groups, of which the most noteworthy are the **smuts, rusts, mushrooms, bracket-fungi, puffballs,** and **coral-fungi.**

Fig. 214. Basidia with spores
A. Basidium.
B. Basidiospores.
C. Hyphal cells.

The smut-fungi (Figure 215) are parasites which cause a number of destructive diseases of higher plants, particularly cereals, such as corn, oats, and wheat. These fungi are called smuts because their spores, which are produced in large quantities, form sooty masses, usually in the developing grains.

The rusts (Figure 216) like the smuts, are all parasites, chiefly upon cereals in which they cause serious diseases which decrease appreciably the yield of infected plants. These fungi are called rusts because, at certain times of their growing period, they form rust-colored blisters on the surfaces of their host plants (Figure 218). The most remarkable biological fact concerning the rusts is the fact that many of them inhabit two unrelated species of hosts, alternating between one host and the other. One of the most destructive and most extensively studied of the rusts is the wheat rust fungus, known botanically as *Puccinia graminis*. The hyphae of this fungus live in the stem and leaf tissues of wheat plants in the summer, during which they produce in surface blisters many one-celled spores called summer-spores, or **uredospores,** which are blown about by winds. If these reach other wheat plants, they infect them and thus spread the disease. In the late summer, the hyphae in the wheat plants begin to form two-celled winter spores, or **teliospores.** These are thick-walled and are quite resistant to low temperatures. They remain dormant on wheat straw and stubble, germinating in the following spring. During this germination, each teliospore develops a basidium which produces 4 basidiospores. These are carried by wind and if they alight on the leaves of the com-

Photo by Benjamin Koehler

Fig. 215. Corn smut (*Ustilago zeae*) on corn tassel.

mon barberry (not to be confused with cultivated Japanese barberries!) they germinate and send hyphae into the leaf tissues. The hyphae on the barberry leaves (Figure 217) form small, flask-shaped structures, called **spermogonia**, on the upper side of the leaves. In these spermogonia, small cells termed **spermatia**, are produced at the tips of hyphae. These cells ooze out to the surface of the leaves in a sweetish liquid which attracts insects. The basidiospores and the hyphae into which they grow are of two physiological types, called plus and minus strains; similarly, the spermatia produced by the hyphae in the barberry leaves are of two types, plus and minus. When a plus spermatium is carried by insects to a minus infection, or vice versa, a plus spermatium fuses with a minus spermatium, following which there develops a mycelium which leads to the production of **aeciospores**. These are shed in spring from small cup-like blisters on the lower surfaces of barberry leaves and are blown to young wheat plants which they infect. The hyphae in wheat plants then form uredospores, and thus the cycle continues. Efforts are made to control rusts in cooler parts of the temperate zones by eradicating common barberry plants. The fungus is unable then to complete its life cycle, for uredospores cannot withstand cold winters

Fig. 216. Black stem rust (*Puccinia graminis tritici*) on wheat stems (left) and barberry leaves (right).

and teliospores which can survive winter temperatures produce basidiospores which cannot infect wheat plants. In more southerly regions with mild winters, the eradication of barberries is not an effective check on the disease, for uredospores can survive the warm winter weather and thus infect wheat plants during the following summer. Under such conditions the fungus is independent of barberry plants for the completion of its life cycle. The wheat rust fungus does tremendous damage to the yield of wheat plants and is considered as one of the most virulent plant parasites. Another common rust is
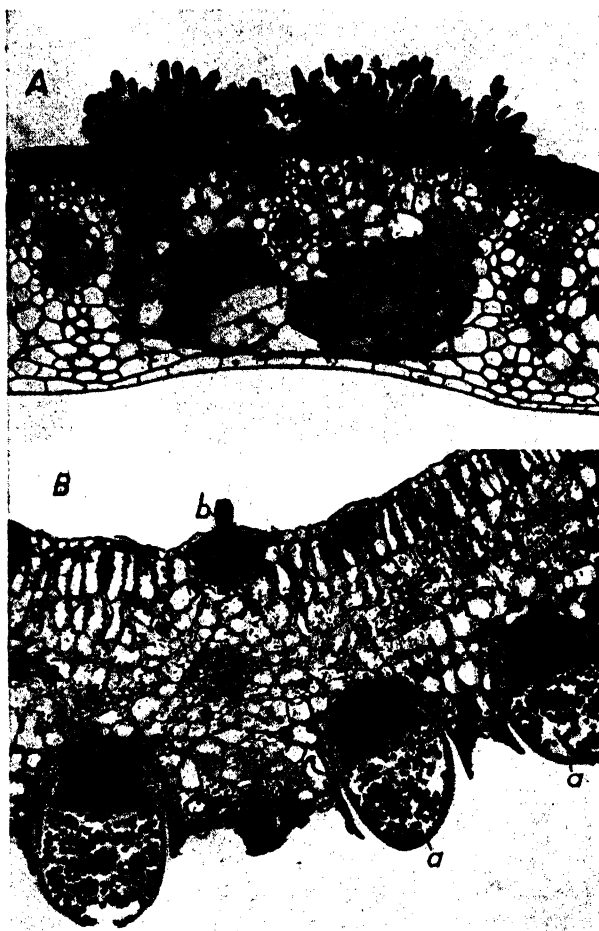
Fig. 217. Wheat rust
A. Teliospores form-
ing on wheat leaf.
B. Spores on bar-
berry leaf.
a. aeciospores in
aecial cups.
b. spermatia in
spermagoni-
um.

*Photo by Triarch Bo-
tanical Products*

cedar-apple rust which lives for a part of the year on cedars, another portion of the year on apples or hawthorns. The white pine blister-rust fungus alternates between white-pine trees and wild gooseberries and currants. It causes serious damage to white pines and may be in part controlled by the eradication of the alternate hosts, the wild gooseberries and currants.

The mushrooms, puffballs, bracket-fungi, and coral-fungi are chiefly saprophytes, living upon decaying organic matter in the soil or upon rotting wood. A few species are parasites on trees.

In mushrooms, the hyphae form extensive growths beneath the sur-face of the soil. When they have collected sufficient quantities of food,

Fig. 218. Orange leaf rust of wheat (*Puccinia tritici*).

they produce the mushrooms, which are the spore-bearing structures of these fungi. Thus, a mushroom is only a part of a large aggregation of hyphae, most of which are subterranean. A mushroom consists usually of a **stalk**, with an expanded umbrella-like **cap**, on the under surface of which are the **gills**, thin plates of tissue which radiate from the center to the edges of the cap like the spokes of a wheel (Figure 219). On the gills are produced the basidia which form the basidiospores. These are carried by wind or insects and germinate into hyphae when they come in contact with favorable conditions (abundant food and

Photo by C. F. Hottes

Fig. 219. A mushroom. Note stalk, and gills on lower surface of cap.

Photo by Missouri Botanical Garden

Fig. 220. Shaggy-mane mushrooms (*Coprinus comatus*).
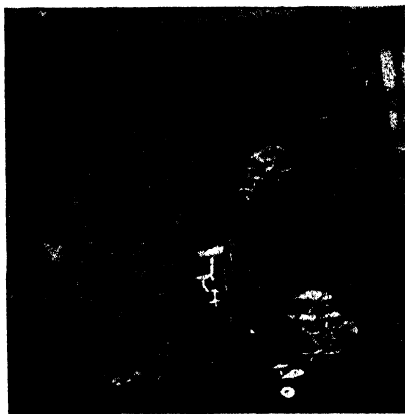
Photo by C. F. Hottes

Fig. 221. Mushrooms on a tree stump.
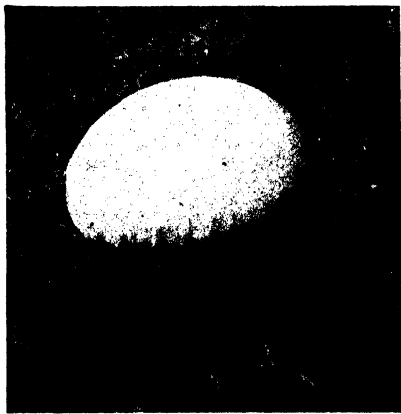
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Fig. 222. A puffball (*Lycoperdon*).

moisture). Mushrooms produce tremendous numbers of spores. A common cultivated mushroom (*Agaricus campestris*) produces, according to estimates, about 1,800,000,000 spores. A shaggy-mane mushroom (Figure 220) is known to release about 100,000,000 spores per hour for several hours. Many mushrooms are edible, others are poisonous ("toadstools"). Despite certain popular formulas for easily distinguishing between edible and poisonous species, the edible mushrooms can

Photo by C. F. Hottes

Fig. 223. Puffballs on rotting wood. Notice the rhizomorphs (compact strands of hyphae) penetrating the wood.

be separated from poisonous forms only by experts who are acquainted with the structure and habits of individual species.

Puffballs (Figure 222) are similar to mushrooms in the structure of their hyphae and basidia and in the subterranean position of most of their hyphae (Figure 223), but they lack gills and bear their spores inside a rather tough outer coat. Puffballs are the most prolific of all organisms in the numbers of reproductive cells produced. A single large puffball has been found to produce 7,000,000,000,000 spores, a number about 58,000 times the population of the United States! Puffballs are usually spherical or pear-shaped. None of the puffball species is deadly poisonous but many of them are too leathery or fibrous to be used as human food. Most puffballs are edible when they are very young and succulent but may become poisonous as they age. Like mushrooms, they are chiefly saprophytes.

The hyphae of bracket-fungi (sometimes called pore-fungi) penetrate the woody tissues of trees (Figure 224), from which they derive food as a result of the digestive action of their exo-enzymes. These hyphae form horizontal, shelf-like growths (Figure 225) on the surfaces of
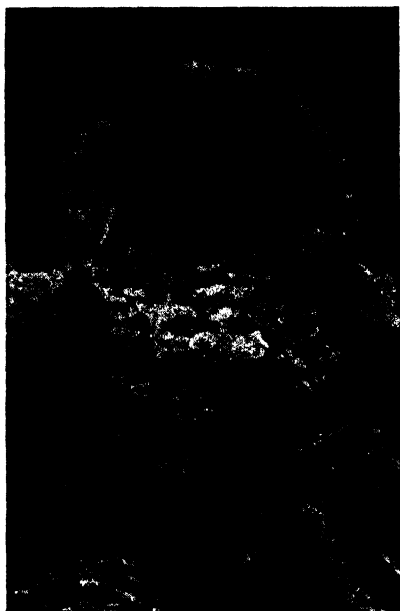
Fig. 224. Shelf fungi on a stump.

Fig. 225. Shelf fungi on a tree trunk.

bark. The "brackets" are the spore-bearing parts of these fungi. Many bracket-fungi are parasites, others are saprophytes which grow only on rotting wood.

The coral fungi, which are related to puffballs, have delicate, much-branched spore-bearing bodies which resemble somewhat masses of coral. They are chiefly saprophytic.

5. LICHENS

Lichens are associations of certain algae and fungi, living together in a state of symbiosis. The algae which are found in lichens are blue-greens and greens; the fungi are chiefly ascomycetes (sac-fungi). The fungi are mildly parasitic on the algal cells, from which they derive food. The fungi recompense the algae by absorbing and retaining water which the algae use in photosynthesis and by protecting the algal cells against desiccation. The fungi and algae in these associations may reproduce independently. The lichens are common on rocks, tree bark (Figure 226), certain soils, and occasionally on the roofs of houses. They vary greatly in color — some are grayish green, others are yel-

lowish-green, yellow, orange, and black. Some species are able to withstand low temperatures and long periods of drought. Such species are very abundant on mountain tops, in arctic tundras, and in many other localities where conditions are so unfavorable as to discourage the growth of other kinds of plants. There are three types of lichens (Figure 227): **crustose lichens,** which form hard, often granular crusts on rocks and bark; **foliose lichens,** which are leaf-like; and **fructiose lichens,** which are more or less erect and much branched.

Some of the lichens are important to man and in nature. Lichens were used by Greeks, Romans and other ancient races as a source of purple and blue dyes. At present, the dye known as litmus, used commonly in chemical laboratories

Photo by R. V. Drexler

Fig. 226. Lichens on a tree trunk.

as an indicator of acidity and alkalinity, is obtained from certain lichens. A few species of lichens, for example, reindeer-moss, are important food plants for deer and other animals in the far north. Some lichens have been used as human food; the manna of Biblical stories was probably a lichen, and at present, Eskimos and Icelanders use certain northern lichens as food plants. Lichens are important in nature in that they secrete organic acids which disintegrate rocks, thus forming soil and preparing substrata in which other kinds of plants can subsequently become established.

Fig. 227. Lichens

Physcia — a crustose lichen. *Usnea* — a fruticose lichen. *Parmelia* — a foliose lichen.

6. SUMMARY

1. The fungi are thallus plants; that is, they lack true roots, stems, and leaves. Their cells show relatively little differentiation, as compared with those of higher plants.

2. The fungi lack chlorophyll and are therefore chiefly parasites or saprophytes.

3. The fungi are a heterogeneous group of plants, the relationships of which are incompletely known.

4. The fungi parallel the algae in many features of their structure and reproduction.

5. The cells of fungi, other than bacteria and a few other species, are organized into fungous threads, or **hyphae**. Some species are unicellular or colonial, but most fungi are multicellular.

6. In the lower fungi, reproduction is entirely asexual. In many higher types both asexual and sexual reproduction occur. Both isogamy and heterogamy occur among fungi.

7. Reproduction in higher fungi is chiefly by means of spores, some asexual, others produced as a result of sexual processes.

8. Since they lack chlorophyll and do not carry on photosynthesis, fungi are able to grow independent of light. Their chief growth requirements are moisture and abundant supplies of organic materials.

9. The sex organs of fungi are unicellular.

10. Lichens are symbiotic associations of algae and fungi.

Plant Diseases

1. THE NATURE OF PLANT DISEASES

PLANTS, LIKE animals, are susceptible to attacks by other living organisms which may live inside them or upon them. The parasitic organisms which invade the tissues of plants and rob them of food or injure them in some other manner are called **pathogens** and the disturbances which they bring about are termed **diseases.** A plant disease may be defined as any abnormal physiological or morphological condition which is of sufficient duration to cause a marked disturbance and which is induced by the attacks of pathogens or by unfavorable conditions, such as deficiencies in soils of essential nutritional elements, or internal physiological aberrations.

The abnormalities which constitute a disease are caused by various types of physiological and morphological derangements within the host. The plundering of food from the tissues of a host plant by the cells of a parasite decreases the stores of material which the host uses in its growth and thus leads to stunting and retardation of growth processes. Parasites frequently form metabolic waste products which are toxic to host tissues and cause their death. Further, the mere presence of parasitic organisms within the tissues of a host often induces abnormalities through simple mechanical effects, as, for example, in certain wilt diseases in which the death of the host is in part a result of the stoppage of conducting cells by masses of bacteria. Parasites frequently secrete considerable quantities of growth substances (auxins) which accelerate the growth of certain cells and produce various types of abnormal enlargements (**hypertrophies**), such as **galls.** The diseases which result from a deficiency of essential chemical elements are obviously attributable to aberrations in the normal physiological activities of the diseased plant; for example, a deficiency of iron or magnesium induces chlorosis, a condition in which chlorophyll fails to develop, a lack of nitrogen, sulfur, or phosphorus hinders the synthesis of proteins, etc. Certain types of plant diseases are associated with

internal physiological derangements, which are often related to external factors. These **physiological diseases** most frequently appear during the storage or shipment of fruits and vegetables, although in some plants they may appear in the fields before harvest. Among the important physiological diseases of plants are bitter-pit of apples, apple scald, tomato scald, and blackheart of potato. Some of these (e.g., bitter-pit) are apparently caused by unbalanced water relations of the plants, others (e.g., apple scald) are caused by the accumulation of certain gaseous by-products of metabolism, and still others (e.g., black-heart of potatoes) are caused by high temperatures and poor ventilation during storage.

The effects which are produced in a diseased plant or part of a plant by such disturbances are termed **symptoms.** These symptoms, which most frequently take the form of morphological alterations, less often of visible physiological derangements, constitute the means by which plant pathologists are able to detect the presence of disease and often to distinguish among various kinds of diseases. Among the common external symptoms of plant diseases are the following:

1. **Wilts,** in which the aerial portions of plants wilt and dry out, sometimes as a result of some interference with the conduction of water in xylem tissues. Examples: wilt diseases of cucumber, watermelon, tomato, potato, and corn.

2. **Scabs** and **blotches,** which are lesions produced by the growth of a pathogen in surface tissues of the host. Examples: apple scab, potato scab.

3. **Hypertrophies,** which are enlargements formed as a result of accelerated growth of the host tissues invaded by a pathogen. Examples: crown gall of alfalfa, clubroot of cabbage, insect galls on leaves and stems, black knot of plum.

4. **Leaf spots,** usually brownish areas of dead tissue killed by parasites present in the leaves. Examples: leaf spot diseases of tomato, rose, and many other plants.

5. **Rots,** soft, discolored masses of tissue, the cell walls of which are destroyed by a pathogen. Examples: soft rot of peaches, bitter rot of apples, rot diseases of strawberries, sweet potatoes, etc.

6. **Cankers,** depressed, dead areas of the surface tissues usually of stems, resulting from infection by bacteria or higher fungi. Examples: fire-blight disease of apples and pears, chestnut blight.

7. **Blights,** the sudden death of blossoms, young leaves and twigs, usually before they are fully developed. Examples: fire blight of pear.

8. **Pustules,** or blisters, formed by the rupture of the surface tissues of a host by spore masses or fruiting bodies of pathogenic fungi.

9. **Hyphae,** or fungous threads which frequently form whitish or grayish patches upon the surfaces of leaves and fruits. Examples: powdery mildews of lilac and clovers.

10. **Chlorosis,** or failure of chlorophyll development, caused by mineral deficiencies or by viruses and certain parasitic fungi.

11. **Mosaics,** or unequal development of chlorophyll in different parts of a leaf, caused chiefly by viruses. Examples: tobacco mosaic, tomato mosaic.

12. **Discolorations,** or the development of unusual colors in the diseased tissues, as in the blackheart disease of potatoes.

The modern scientific study of plant diseases is a branch of botanical science which began with the demonstration in 1853 that fungi are able to live parasitically in the tissues of green plants. The work of the famous French bacteriologist, Louis Pasteur, upon animal diseases, was an important factor in stimulating interest in plant diseases, the study of which expanded rapidly in the last quarter of the nineteenth century and has grown into the extensive modern science of **plant pathology.** A significant event in the history of plant disease study in the nineteenth century was the discovery by Professor T. J. Burrill, working on the fire-blight disease of pears, that parasitic bacteria cause plant disease, a fact previously denied by bacteriologists. Research upon plant disease problems is conducted chiefly by various governmental agencies, such as the United States Department of Agriculture which maintains a large staff of plant pathologists in centralized laboratories and also in the fields in which crop plants are grown. Plant pathological research is also conducted by the larger universities and private commercial organizations, chiefly those which manufacture spray chemicals for controlling diseases. These institutions study all aspects of plant diseases — causes, symptoms, control and eradication, fluctuations from year to year, resistance and susceptibility of various host species and varieties to disease, disease migrations, the breeding of disease-resistant varieties of crop plants, etc.

2. THE CAUSES OF PLANT DISEASES

As indicated in the preceding section of this chapter, the causal agents of plant disease can be grouped into four general categories: first, **pathogenic organisms,** second, **chemical agents,** third, internal

Fig. 228. Corn smut caused by *Ustilago zeae* on ear of corn.

physiological disturbances, and fourth, **viruses.** Of these the biological agents and viruses are responsible for the greater number of the diseases of higher plants and are generally the more difficult to control. The chemical agents, some of which bring about diseased conditions when they occur in excessive quantities, others of which induce abnormalities when their amounts are deficient, are ordinarily more easily controlled, usually by increasing or decreasing the concentrations of the chemical substances responsible for the diseased conditions. The physiological diseases of certain plants can be controlled in part by proper manipulation of storage temperature and by providing adequate ventilation during storage.

The principal agents responsible for many diseases of flowering plants are outlined below:

1. **Bacteria,** which cause the following important diseases: fire blight of pears and apples, wilt diseases of corn, cucumbers, melons, potatoes, tomatoes, and squash, crown galls of apple, alfalfa, raspberry, and grape, bacterial blight of beans, soft rot of carrot and other vegetables, citrus canker, bacterial blight of walnut, and many others.

2. **Higher fungi,** responsible for many of the diseases (Figures 229, 230) of economically important plants. Among these diseases are the rusts and smuts (Figure 228) of cereals, bitter rot of apples, apple scab, Dutch-elm disease, chestnut blight, potato blight, downy mildew of grape, brown rot of peaches, peach-leaf curl, and anthracnose of beans.

3. **Parasitic flowering plants,** such as mistletoes (Figures 231, 233) and dodders (Figure 232), attack many autotrophic flowering plants, such as legumes, pines, oaks, Douglas fir, hemlock, apple, juniper, and many other host species.

4. **Animals.** The round worms, or **nematodes,** attack frequently the roots, and often the leaves and stems of numerous host species, causing the nematode diseases of wheat, rye, clover, begonia, tomato, cotton, sugar beets, peony, tobacco and many other kinds of flowering plants. **Insects** are important not merely as carriers of plant disease organisms, but are directly responsible, as a result of their chewing, boring, egg-laying and sucking activities, for the formation of galls and other serious disturbances in the tissues of higher plants (Figures 234, 235, 236, and 237).

5. **Viruses,** the exact nature of which is unknown, are thought by some botanists to be invisible, primitive kinds of living organisms, by others to be expressions of internal physiological derangements, due possibly to unbalanced

Fig. 229. Smut diseases of barley

A. Healthy barley spike.
B. Covered smut of barley (caused by *Ustilago hordei*).
C. Loose smut of ·barley (caused by *Ustilago nuda*).
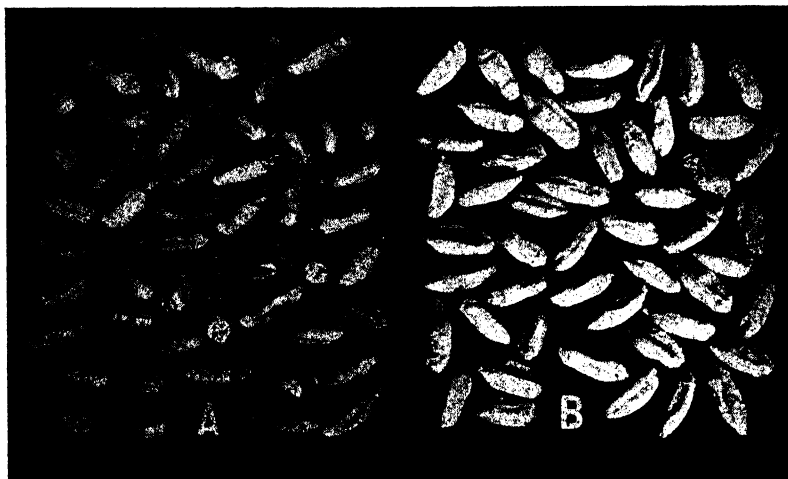
Photo by Benjamin Koehler

Fig. 230. Effect of wheat-scab disease on wheat grains

A. Healthy grains. B. Diseased grains, shrivelled by the disease.

Fig. 231. Mistletoe growing on an Osage orange tree.

Fig. 232. Dodder, a flowering-plant parasite, growing on *Vernonia*.

nutritional relations, abnormal activity of enzymes, or disturbances in the genes of the diseased plant. The viruses are responsible for a large number of important plant diseases, among which are tomato mosaic, potato mosaic, potato leaf roll, mosaic disease of cucumbers, muskmelons, and other members of the melon family, curly top of beats, alfalfa, cabbage, radish, turnip and other plants, the "yellows" disease of peach, and numerous others.

6. **Chemical agents** of toxic nature which cause injury to and sometimes the death of plants or plant parts. Gases

Photo by Missouri Botanical Garden
Fig. 233. Mistletoe, a flowering-plant parasite, growing upon a tree branch.

which are poured into the atmosphere from the burning of coal and combustion processes in smelters and other industrial establishments frequently induce pronounced injury in plants. Sulfur dioxide and other smoke gases, escaping illuminating gas, soot, and other gaseous or solid materials in the air are common causes of plant diseases (Figure 238). Also, certain chemicals in the soils, such as selenium, lead, mercury compounds, etc., exert deleterious influences upon plants, and the arsenic, copper, and other substances in sprays frequently produce injuries which may be considered as diseases. These chemically induced diseases are important not only because of the direct damage caused in plants, but also indirectly in that the damaged areas which they produce are frequently the avenues of entrance of pathogenic fungi.

7. **Chemical deficiencies** result in derangements, as pointed out earlier in this chapter, because of the lack of certain nutrient elements, such as iron, magnesium, sulfur, etc. Deficiencies in essential elements may induce weakness in a host and thus allow pathogens to develop in the host tissues, and sulfur gases in the air bring lesions through which parasitic fungi may freely enter the internal tissues of a host.

In many diseases, several of these factors may be involved simultaneously in the production of disease symptoms. Sugar beets, for example, often suffer from nematodes and curly top disease at the same time.

Photo by Missouri Botanical Garden

Fig. 234. Insect galls on hickory leaves.

Photo by Missouri Botanical Garden

Fig. 235. Insect galls on oak leaves.
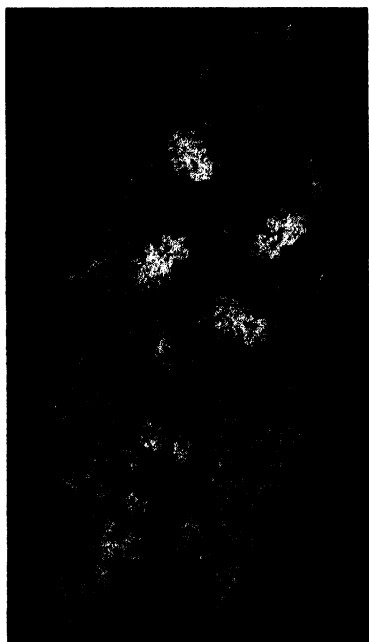
Photo by Missouri Botanical Garden

Fig. 236. Lace-bugs on *Aster* leaves.

Photo by Missouri Botanical Garden

Fig. 237. Injury by flat-headed borers
to trunk of maple.

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Photo by Missouri Botanical Garden

Fig. 238. Smoke-gas damage to water-lily leaves.

3. THE TRANSMISSION OF PLANT DISEASES

That plant diseases frequently spread rapidly over wide areas constitutes a problem of great biological interest and of tremendous economic value. The diseases which are transmitted from plant to plant over extensive areas are chiefly those diseases which are caused by pathogenic fungi and viruses. Obviously, diseases which are caused by excesses or deficiencies of certain chemical substances are related entirely to local conditions of the atmosphere and the soil, conditions which are peculiar to a given region. Such diseases are thus not transmitted, for they depend upon passive factors in the immediate vicinity of the diseased plants.

The principal agencies which transmit plant diseases carry the spores or other reproductive structures of pathogenic organisms from plant to plant, or in some cases, transport entire, unicellular pathogens or virus substances. The chief agencies of disease transmission are:

1. **Wind,** which may carry spores of fungi through very great distances.

2. **Water,** which in streams and lakes frequently transports fungous spores and bacteria.

3. **Insects,** which carry fungous spores and bacteria and which are the principal carriers of viruses.

4. **Birds,** which transmit spores, bacteria, and also viruses.

5. **Man,** who in his migrations and in his traffic in plant products has unwittingly been an important agent in the spread of plant diseases.

Of these agencies, wind and insects have been probably most effective in the transmission of plant disease organisms and viruses in rather limited areas. Man has been the chief transgressor in spreading diseases over wide areas of the earth.

4. THE RELATION OF PLANT DISEASES TO ENVIRONMENTAL CONDITIONS

The diseases of plants are markedly influenced by conditions of the soil and atmosphere in which plants grow. In some cases, factors of the external environment are directly responsible for plant diseases, as mentioned earlier in this chapter; the blackheart disease in potatoes is attributable to high temperatures and poor ventilation during storage, the bitter-pit disease of apples is a result of disturbed water relations, etc. Environmental factors also frequently exert indirect influences upon plant diseases, chiefly through the effects of temperature and moisture conditions upon the host plants or upon the parasitic organisms causing the diseases. It has been often observed that the severity of various plant diseases fluctuates considerably from year to year, a fact which is explained principally by seasonal variations in environmental conditions. For example, the bacterial wilt disease of sweet corn is usually much more severe in a summer which follows a mild winter than during a season following a very cold winter. Also, the potato scab disease is usually more severe when the host plants are growing in an alkaline rather than in an acid soil. The apple scab disease is favored by rather damp, cool weather; the asci in fallen leaves discharge their ascospores only when the leaves are wet, and new leaves on apple trees can be infected by apple scab spores only when they are wet. Varying environmental factors thus influence not only the physiological activities and degree of disease resistance in host plants, but also they exert important effects upon the rate of growth and virulence of pathogenic organisms, the rate of spore production, the dispersal of spores, and also the germination of spores.

5. THE CONTROL OF PLANT DISEASES

One of the major objects of plant pathologists is to devise effective methods of combating plant diseases, either by holding them in check, or, if possible, by eradicating them completely. The treatment of plant diseases differs in one fundamental way from the manner in which a

physician treats human disease, or a veterinarian treats sick animals. Plant pathologists, in attempting to control the diseases of plants, are interested in the protection of plants as a mass of organisms growing in vast numbers, in a particular field or orchard, for example, or over an area of many square miles, whereas physicians and veterinarians are concerned primarily in the treatment of individuals. The methods of treating plant and animal diseases are necessarily somewhat different because of the morphological and physiological differences between plants and animals, but their object is the same — the prevention of disease by restraining or elimi-

Photo by Missouri Botanical Garden

Fig. 239. Spraying trees to kill parasites.

nating the causes of disease and the curing of diseased organisms by destroying or inhibiting the causative agents, without injuring the diseased plant or animals.

The principal methods employed in the control of plant diseases are these:

1. **Spraying** (Figure 239) or **dusting** — the application of liquid or powdered chemical preparations to the parts of plants which are diseased or likely to become diseased. Common ingredients of sprays and dusts are copper and sulfur, used to combat fungi; lead, nicotine, and arsenic, used chiefly to control insects; and various other chemicals, which kill many kinds of pathogens but which, under carefully controlled conditions, cause little or no injury to the host plants.

2. **Seed treatment** — the soaking of seeds for brief periods of time in solutions of chemicals which kill the spores of higher fungi or bacteria which may adhere to the coats of seeds. Common ingredients in such solutions are formaldehyde and mercury compounds, which kill spores and bacteria quickly without injuring the seeds, provided the latter are not allowed to remain too long in the solutions.

3. **Eradication** — the removal and destruction of infected plants to prevent the spread of diseases to healthy plants. In the rusts, about 10 percent of the species of which alternate between two hosts, the diseases which they produce can be effectively controlled in certain regions by eradicating all plants of the less important host species, so that the fungi cannot complete their life cycles. The eradication of common barberries, for example, controls the wheat rust disease effectively in some regions.

4. **Checking insect carriers** — the reduction in numbers or destruction of the insects which carry disease-producing agents, such as bacteria, fungous spores, and viruses. This is the only effective method in checking virus diseases.

5. **Quarantine** — the regulation of traffic in plants between areas with certain diseases and other areas in which those diseases have not yet appeared. Federal and state plant quarantine workers are stationed at ports of entry along national and state borders and inspect plants and plant materials brought to such borders. Some plants may be permitted to cross these borders if they are disease-free; others may be transported across after they are treated to destroy any parasites which might be present upon them, and still others are allowed under no conditions to pass certain borders. The quarantine method of control has been moderately effective in preventing the spread of various diseases.

6. **Breeding of resistant varieties of crop plants** — a method of eliminating the destructive effects of certain diseases by breeding new varieties of crop plants which are resistant to particular diseases. This method of control has been singularly effective in many species of plants.

One of the serious problems which plant pathologists face is the fact that fungous species, like higher plant species, vary a great deal, some individuals of a species being more vigorous and more virulent than others. As a result of this variation and also of hybridization and mutation among fungi, new races or strains of fungi are continually appearing, just as new types of plants develop among higher plant species. Thus, plant pathologists by cross-breeding and selection may develop resistant varieties of host plants, only to discover, subsequently, that fungous races have appeared to which the "resistant" varieties of crop plants are no longer resistant. As resistance varies among host varieties, so virulence varies among pathogens; thus it is impossible to develop varieties of crop plants which remain permanently resistant to particular fungous diseases.

6. THE ECONOMIC IMPORTANCE OF PLANT DISEASES

The actual kinds of injury caused by plant diseases and responsible for the undesirability of diseased plant produce are varied. Some diseases cause flowers, fruits, and other parts to become stunted, malformed, or discolored so that they become unfit for commercial use. Other diseases, such as barley scab and ergot of oats, render the products derived from the host plants distasteful or poisonous; these may cause serious illness or death of human beings or their domesticated animals. Another of the effects of plant diseases is to reduce crop yield to such an extent that the cultivation of certain crops may become economically unprofitable.

The crop losses caused by plant diseases are staggering in their magnitude and thus constitute a serious economic and agricultural problem. The following table presents the estimated reductions in the yields of certain crops, caused by important plant diseases in 1938, a normal year from the standpoint of plant disease losses, in the United States; the data in this table were compiled by the Plant Disease Survey of the United States Department of Agriculture and represent estimates only. In 1938, however, these estimates were actually somewhat lower than the observed losses from the respective diseases.

Disease	Estimated Reduction in Yield
Wheat stem rust	85,452,000 bushels
Wheat loose smut	5,995,000 bushels
Barley stem rust	12,046,000 bushels
Oat loose smut	32,728,000 bushels
Field corn smut	95,087,000 bushels
Field corn bacterial wilt	1,342,000 bushels
Field corn — all diseases	335,826,000 bushels
Sweet corn smut	33,221 short tons
Irish potato late blight	7,141,000 bushels
Irish potato — all diseases	58,673,000 bushels
Cotton fusarium wilt	374,000 bales
Tobacco downy mildew	81,502,000 pounds
Cherry leaf spot	8,111 tons
Apple scab	12,774,000 bushels
Strawberries — all diseases	746,000 crates
Grape black rot	15,915 tons
Peach brown rot	1,492,000 bushels

SUMMARY

1. A plant disease is an abnormal condition which is of sufficient duration to cause a marked disturbance and which is induced by the attacks of pathogens or by unfavorable external conditions or internal physiological aberrations.

2. The disturbances caused by diseases are due to the removal of food from the host by the pathogen, to the formation of toxins by the pathogen, to mechanical effects of the presence of the pathogen, to a deficiency of essential mineral elements, to various physiological derangements induced by unfavorable external conditions, etc.

3. Diseases caused by disturbed physiological relations are termed physiological diseases.

4. The characteristic effects produced in a diseased plant are called symptoms. The most common visible symptoms of plant diseases are: wilts, scabs and blotches, hypertrophies, leaf spots, rots, cankers, blights, pustules, chlorosis, the presence of hyphae, mosaics, etc.

5. The causes of plant diseases are:
   a. pathogenic organisms: bacteria, higher fungi, parasitic flowering plants, animals, etc.
   b. chemical agents: poisons, chemical deficiencies, etc.
   c. internal physiological disturbances.
   d. viruses.

6. Plant diseases are transmitted by:
   a. winds.
   b. water.
   c. insects.
   d. birds.
   e. man.

7. The virulence of plant diseases and the rapidity of their transmission vary with changes in environmental conditions.

8. The principal methods of eradicating or controlling plant diseases are:
   a. spraying or dusting
   b. chemical treatment of seeds
   c. eradication of diseased plants
   d. checking insect carriers
   e. quarantine
   f. breeding disease-resistant crop plants

9. The chief economic importance of plant diseases lies in the fact that they destroy plant products or render them unusable, or decrease yields so that agriculture becomes unprofitable.

Bryophytes: Liverworts and Mosses

THE BRYOPHYTES are the first true green land plants met with in our survey of living plants. They are small and inconspicuous, rarely achieving more than a few inches of height or length. Some of them have typical thallus bodies and others have primitive stem- and leaf-like structures. True roots are not present in bryophytes, but simple hairs called **rhizoids** penetrate the soil, anchor the plants, and absorb water and minerals from the soil. Although they function in the same manner as roots, rhizoids are not structurally roots because they are hairs and lack the characteristic anatomical features of roots. Despite the fact that they are land plants, the bryophytes are mostly restricted to moist, shaded habitats, for they require water for fertilization and most of them are quickly dried out by the sun if they are not in very humid places. The sex organs of bryophytes are many-celled structures; the female sex organs (**archegonia**) are pear-shaped and each contains a single egg. Each archegonium has an enlarged, hollow base (**venter**) within which an egg is formed. From this swollen base there arises an elongated **neck,** through which there develops at maturity a **canal,** extending from the open mouth of the archegonium to the globose egg cavity. This canal results from the disintegration of certain cells in the neck. The male sex organs (**antheridia**) are ovoid or spherical and each produces numerous sperms. Multicellular sex organs represent an important evolutionary advance, for they offer more protection to gametes and zygotes than do one-celled sex organs such as those of thallophytes.

Alternation of generations occurs in all bryophytes. The gametophyte in all species is the conspicuous, dominant generation, and the sporophyte is much smaller and less complex structurally than the gametophyte. It is dependent for its nourishment upon food manufactured by the gametophyte. All bryophytes contain chlorophyll and can thus manufacture their own food.

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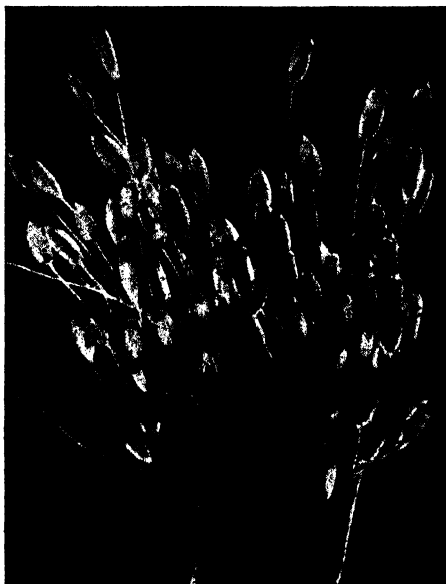
Fig. 240. Moss sporophytes (*Polytrichum*).

There are approximately 23,000 known species of bryophytes. These are subdivided into liverworts and **mosses.**

1. LIVERWORTS (HEPATICAE)

The liverworts grow in moist shady locations, in soil, on rocks, and occasionally on the bark of trees. They are especially common on limestone cliffs in humid localities. Most liverworts have a thallus body which grows flat upon their substrata (Figure 241). A single liverwort thallus is a somewhat branched, ribbon-shaped structure which rarely exceeds three or four inches in length and three-fourths of an inch in width. From the lower surface of the thallus grow the rhizoids which vary from one-fourth to one inch in length. These hold the thallus fast to the substratum and absorb water and minerals. Some of the liverworts, called leafy-liverworts, are more or less erect and bear tiny, leaf-like structures which resemble the so-called leaves of mosses. A liverwort plant, as described above, is the gametophyte generation of its species. It produces archegonia and antheridia which bear respectively eggs and sperms. In some liverworts the sex organs are embedded in the tissues of the thallus, in others they are borne on special stalks which rise above the surface of the thalli. In the presence of water, sperms swim to the archegonia which they enter. A sperm fertilizes an egg inside an archegonium, and the zygote thus formed begins its development *inside the archegonium*. This feature is very different from the condition in thallophytes, in which zygotes ordinarily escape from the cells in which they are formed and germinate outside of their parent plants. The retention of the zygotes and developing sporophyte inside the archegonium is an important evolutionary advance which is correlated with development of a land habit. The zygote and young sporophyte, held within the archegonium, are protected by the tissues of the

Fig. 241. Liverwort plants (*Marchantia polymorpha*). Note the gemmae cups.

latter against desiccation and mechanical injury and are nourished by the tissues of the gametophyte, which surround them. This nutrition of the sporophyte by the gametophyte generation persists throughout the lives of sporophytes of mosses and liverworts. In higher groups of plants, as will be described later, the zygote and sporophyte are held and nourished by the gametophyte for only a short time, until they grow sufficiently to produce their own food-making organs (leaves). Then they achieve nutritional maturity and become independent of the gametophyte, which then usually disintegrates. The zygote of a liverwort grows into the diploid sporophyte generation, which consists chiefly of a spore-producing capsule and of tissues which fasten it to the inner part of the archegonium from which it develops. The sporophytes of liverworts vary in size; in some species they are but a small

Fig. 242. Thallus of a liverwort, *Marchantia*, showing gemma cups.

fraction of an inch in length, in others they may reach a length of four or five inches. In the developing capsule of the sporophytes, reduction division occurs in the process of spore-formation; the spores formed by such divisions are thus haploid and constitute the first stage of the gametophyte generation. When the capsule is mature, it splits open and liberates the spores which fall to the ground or are blown about by winds. If they come in contact with favorable conditions, the spores germinate, each growing eventually into a thallus, which then forms archegonia and antheridia, leading to the formation of another sporophyte generation (Figure 243). In some liverworts, archegonia and antheridia are borne on the same thallus, while in other species (Figure 244), archegonia are borne on certain thalli, antheridia on others. Many liverworts bear on their upper surfaces small cup-shaped growths known as **gemma cups,** within which are produced small, flattened, oval structures called **gemmae.** When separated from the parent gametophyte, the gemmae are able to grow directly into new thalli (Figure 242). Reproduction by means of gemmae is strictly an asexual, vegetative type of multiplication, comparable with reproduction by means of rhizomes, runners and other vegetative organs in seed plants. Since gemmae are produced from gametophyte tissue; their cells contain the haploid chromosome number.

The importance of liverworts to man and in nature is insignificant. They probably furnish small quantities of food for certain animals and are of some importance in breaking the force of raindrops and thus preventing soil erosion. Some of them are apparently early colonizers of rock slopes and other kinds of terrain which other types of plants are not able to inhabit.

Fig. 243. Liverworts

A. Thallus of *Conocephalus*, with two archegonial stalks. The older stalk bears three tiny sporophytes beneath its umbrella-shaped cap.
B. Thallus of *Marchantia*, with antheridial stalks.
C. Thallus of *Màrchantia*, with young antheridial stalks.
D. Thallus of *Marchantia*, with mature archegoniate stalks, bearing young sporophytes on the undersurfaces of the ribs.
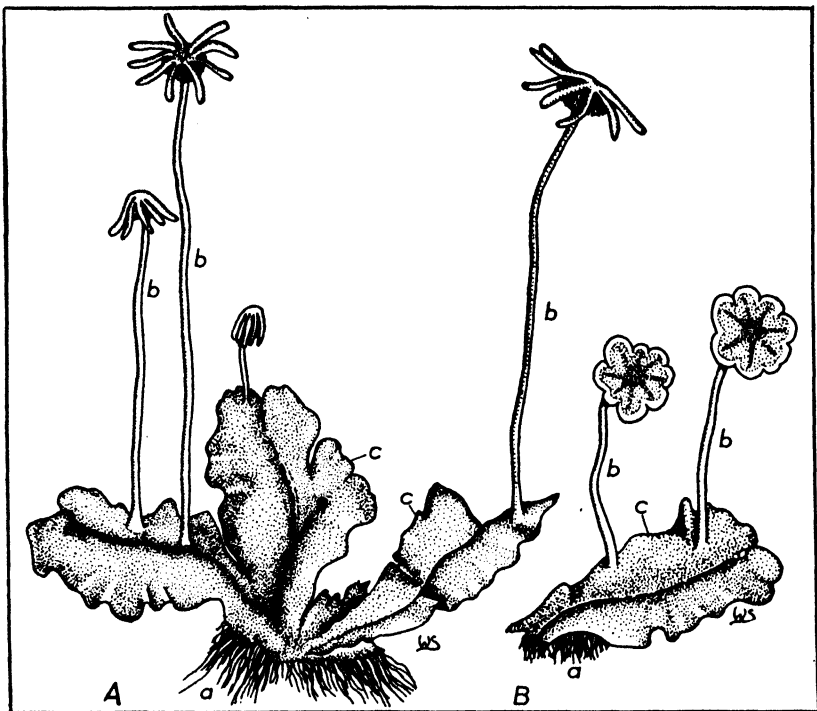
Fig. 244. Plants of *Marchantia*

A. Archegonial plants: a. rhizoids, b. archegonial stalks, c. thallus.
B. Antheridial plants: a. rhizoids, b. antheridial stalks, c. thallus.

2. MOSSES (MUSCI)

Mosses are more numerous than liverworts, both in numbers of species and numbers of individuals. Mosses are generally erect or nearly so, in contrast to the flat, creeping habits of many liverworts. They rarely exceed heights of 6 or 7 inches. The body of a typical moss plant is composed of an erect stem-like portion, with rhizoids growing from its basal end into the soil and with small, green "leaves," or leaf-like structures along its axis (Figure 245). Mosses are thus somewhat more complex structurally than liverworts, but, like liverworts, they lack differentiated vascular tissues. A few species of mosses have elongated, somewhat specialized conducting cells in their stems, but these cells are simple and vastly different morphologically from the conducting cells of seed plant stems. The moss plant composed of simple stem and leaves and of rhizoids is the major part of the gametophyte generation.

At the apex of the leafy shoot of a moss plant are borne the sex organs, usually surrounded by close-growing leaves and interspersed with sterile filaments of cells (Figures 246, 247). In some species of mosses, the antheridia and archegonia are borne at the apex of the same shoot, in other species, they are produced on separate plants. The sex organs and gametes of mosses are quite similar to those of liverworts. As in liverworts, fertilization is absolutely dependent upon liquid water, either in the form of rainfall, running water, or films of dew. When mature antheridia are wetted, they liberate their sperms which swim through water films, or are splashed by rainfall, until they reach the archegonia. Several sperms enter the mouth of an archegonium and swim down its canal to the egg. As in liverworts, only a single sperm fertilizes the egg. The zygote thus formed grows by cell division into a young sporophyte, which, like the sporophyte of a liverwort, is attached to the gametophyte plant by means of its connection (a mass of tissue called the foot) with the archegonium. The sporophyte continues to
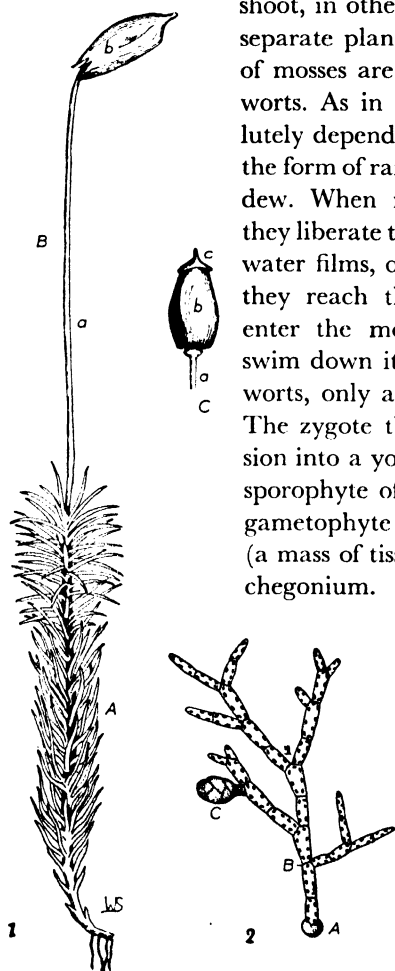
Fig. 245. 1. Moss plant

A. "Leafy" shoot (gametophyte).
B. Sporophyte: a. stalk, b. capsule.
C. Enlarged capsule: a. stalk, b. capsule, c. lid.

2. Moss protonema

A. Spore case.
B. Protonema cells.
C. Bud.

grow and ultimately matures into a slender **stalk** with an enlarged **capsule** at its apex (Figure 240). This stalk varies in length from a small fraction of an inch to 5 or 6 inches. The capsule contains cells which, by reduction division, form spores. The elongated sporophyte of a moss has an advantage over the shorter sporophyte of most liver-

Fig. 246. Apices of moss leafy shoots
A. Apex of female shoot, showing archegonia, "leaves," and sterile hairs.
B. Apex of male shoot, showing antheridia, "leaves," and sterile hairs.

worts in that it holds the spore case well into the air and thus facili-
tates the dispersal of spores by wind. The sporophyte of a moss, like
that of a liverwort, is nourished throughout its existence chiefly by food
which it absorbs from the gametophyte tissues in which its base is
embedded. The sporophytes of most mosses contain some chloro-
phyll, but in insufficient quantities to render them nutritionally inde-
pendent.

The spores, which are haploid, are the first structures of the game-
tophyte generation. A spore under suitable conditions of moisture,
temperature, and soil, germinates and forms a green, branching fila-
ment, the **protonema,** which grows on the surface of damp soil and
resembles a green alga. After a period of growth and photosynthetic
activity, the protonema develops buds, each of which may grow into
an erect leafy shoot, which develops rhizoids at its base and, after a
time, forms sex organs at its apex. Thus the life cycle is completed.

Economically and in nature the mosses are more significant than
liverworts. Most important of the mosses are the peat mosses (*Sphag-
num*), which form extensive mats of vegetation in swamps and bogs.
The accumulation of dead peat moss plants through the ages has
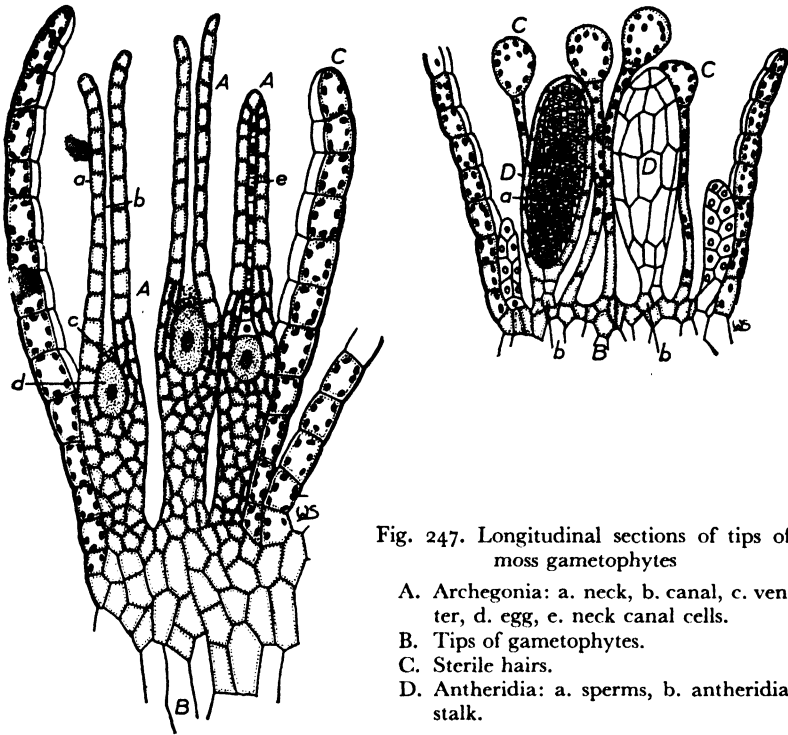
Fig. 247. Longitudinal sections of tips of
moss gametophytes

A. Archegonia: a. neck, b. canal, c. ven-
ter, d. egg, e. neck canal cells.
B. Tips of gametophytes.
C. Sterile hairs.
D. Antheridia: a. sperms, b. antheridial
stalk.

formed **peat,** a deposit rich in carbon. Peat is burned in many parts
of the world, including some of the northeastern United States, as a
fuel. Dried peat moss is used by florists for packing cut flowers, for its
leaves hold water very tenaciously. Sterilized dried peat moss has been
used successfully as an absorbent material in bandages, particularly
during wars when cotton has been scarce. Chopped and ground peat
moss is frequently added to garden soils to increase their water-holding
capacity and to keep them loose and prevent their caking. The dense
masses of vegetation formed by certain mosses gradually fill in small
ponds and lakes and thus aid in the formation of soil, in which higher
types of plants can grow. Mosses are of some importance in breaking
the force of rain and in the prevention of soil erosion. Some of them
apparently serve as food for various wild animals.

Mosses grow in moist habitats—in tropical rain forests as well as in
the cooler regions of the temperate zones and the cold expanses of
sub-arctic tundras. Many of them grow as terrestrial plants with their
rhizoids firmly anchored in the soil, whereas other species grow as

epiphytes upon the branches and twigs of trees and upon the roofs of buildings, upon telephone poles, and other man-made structures, particularly in the tropics.

3. SUMMARY

1. Bryophytes are the most simple structurally of all living green land plants. Their delicate nature and their dependence upon water for fertilization limit most of them to humid habitats.

2. Alternation of generations occurs in all bryophytes. The dominant, more complex, food-making generation is the gametophyte. The sporophyte is smaller and simpler structurally and depends throughout its existence upon the gametophyte generation for its food.

3. The sporophyte generation begins with zygote formation and ends at the time of reduction division. The spores, which result from reduction divisions, develop into the gametophytes which bear the sex organs: archegonia and antheridia.

4. The sex organs of bryophytes are multicellular; the male sex organs are called antheridia, the female, archegonia.

5. The sperms of bryophytes are ciliated and are able to reach the eggs only by swimming through water.

6. The zygote develops inside the archegonium and the sporophyte which it produces is attached to the inner part of the archegonium.

7. The liverworts are chiefly flat and thalloid, the mosses mainly erect and leafy.

8. Because of their dependence upon water and because of certain similarities which they have with green algae, bryophytes are generally considered as having evolved from aquatic ancestors similar to green algae.

9. The bryophytes are considered rather specialized and yet primitive types of land plants which have not developed into more complex plants. Their lack of vascular tissues has placed limitations upon the sizes which they attain, and their dependence upon water for fertilization and their inability to conserve water effectively render most of them unfit for life in any except moist localities.

Pteridophytes: Ferns and Fern Allies

THE PRESENT-DAY pteridophytes number slightly more than 9,800 species. In past ages of the earth's history there were probably more individuals and kinds of pteridophytes than are now living, as is shown by the great variety of pteridophyte fossils found in rock strata. Many of the pteridophytes which were the earth's dominant plants during the Coal Age are now extinct and are known to us only through the fossils which they have left. Some of these now-extinct plants were trees of considerable size, whereas our modern pteridophytes are chiefly small plants rarely exceeding a few inches or a few feet in height, except for some species of tree ferns which grow in humid, tropical forests.

Pteridophytes differ from bryophytes chiefly in that they have well-differentiated vascular tissues, very similar to those of seed plants, and in that their sporophytes are larger and more complex morphologically than their gametophytes, a situation which is the reverse of that in bryophytes. The gametophytes of most ferns and their allies are small and thalloid; they contain chlorophyll and thus, as in bryophytes, are nutritionally self-sustaining. The sporophytes of the ferns and their relatives, with their roots, stems, and leaves, are also green and are nutritionally independent, except for a very brief early period during which they are nourished by the gametophytes from which they develop. This physiological relationship between sporophytes and gametophytes in the pteridophytes is very different from that in the bryophytes, in which the sporophyte generation is wholly or largely dependent for its food upon the gametophyte throughout its life.

The vegetative organs of the sporophytes of pteridophytes contain differentiated xylem and phloem tissues and exhibit other types of cellular differentiation. The arrangement of these various tissues is usually somewhat different from that of modern seed plants; but there are certain similarities with seed plants in anatomical features, particularly in the structure of the leaves of certain pteridophytes.

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Photo by Missouri Botanical Garden

Fig. 248. Plant of a fern (*Asplenium ebenoides*), showing rhizomes and leaves with sori on their under-surfaces.

As in bryophytes, the sperms of pteridophytes are able to reach the eggs in the archegonia only by swimming through liquid water. Thus, pteridophytes are able to reproduce sexually only in localities in which liquid water at some time or other reaches the gametophyte generation. Liquid water in the form of heavy layers of dew or in the form of rain or standing water provides the medium through which the sperms may swim. The well-developed strengthening and conducting tissues of pteridophytes have enabled them to achieve greater sizes than those in bryophytes. Many pteridophytes, however, despite their efficient conducting systems, have thin, poorly cutinized leaves which lose water rapidly. These species, like most bryophytes, are usually limited in their distribution to rather humid, shaded habitats in which the evaporating power of the air is low. Thus, many pteridophyte species are found in damp, tropical forests, and in shaded, moist localities in deep woods, ravines, and thickets in the temperate zones.

The modern pteridophytes are divided into three major groups: **ferns, horsetails,** and **club-mosses.**

1. FERNS (FILICINAE)

The ferns include the largest of the present-day pteridophytes. They reach their greatest development in the tropics, but are also represented in the temperate zones, chiefly in moist regions.

A mature fern plant consists of roots, a stem, and leaves (Figure 248). In most temperate zone and many tropical ferns, the stems are horizontal and grow at or below the surface of the soil. Such stems are

termed **rhizomes.** The tree-ferns of the tropics have erect stems which frequently reach heights of 35 or 40 feet (Figures 250, 252). In the ferns with underground stems, only the leaves and the stem tips normally appear above the surface of the ground. The roots of ferns branch profusely and anchor the plants in the soil; they absorb water and mineral salts which pass through their vascular tissues into the stems, and ultimately the leaves. The leaves of ferns are usually pinnately compound, sometimes doubly compound.

The leaves of most ferns perform two groups of functions: vegetative and reproductive. The leaves are green and carry on photosynthesis, as well as

Fig. 249. Walking fern (*Camptosorus rhizophyllus*). Note new plants developing from tips of leaves which have touched the soil.

digestion, assimilation, respiration, and other vegetative processes. In addition the leaves of ferns produce spores, the reproductive structures of the sporophyte generation. These spores are borne in spore cases, or **sporangia,** which usually develop in small brownish or yellowish clusters called **sori** (singular **sorus**). The sizes, shapes, numbers, and arrangements of sori on fern leaves are important characters used to distinguish among the various genera of ferns (Figure 251). The most common type of fern sporangium is a somewhat flattened structure borne at the end of a slender stalk; seen from the side, it is nearly circular in form; its wall is composed of a single layer of cells, most of which are thin-walled (Figure 253). Some of these cells have unequally thickened walls and form a ring, called the **annulus,** which extends approximately two-thirds of the way around the sporangium (Figure 254). When a sporangium approaches maturity, it dries out and its annulus curves back very slowly, as a result of the unequal drying of its walls, tearing open the sporangium. The annulus then springs forward rapidly thus flinging out the spores, which fall to the ground.

Fig. 250. Young tree ferns, Jamaica.

The spores are haploid, as are those of bryophytes, and thus belong to the gametophyte generation. A spore, if conditions are suitable for its growth, germinates and by cell division forms the principal part of the gametophyte generation, the **prothallus** (Figure 255). A prothallus is a green, thalloid structure which resembles very strikingly a liverwort thallus. It is a flat, thin, heart-shaped structure, which rarely exceeds ¼ of an inch in diameter and which produces rhizoids on its lower surface (Figure 256). These rhizoids anchor the prothallus to the soil and absorb water and mineral salts. Also on the lower surface are archegonia and antheridia, the archegonia near the notch of the heart, the antheridia usually at some distance from the notch scattered among the rhizoids. The antheridia and archegonia are fundamentally like those of bryophytes, except that they are smaller than those of the

A   B
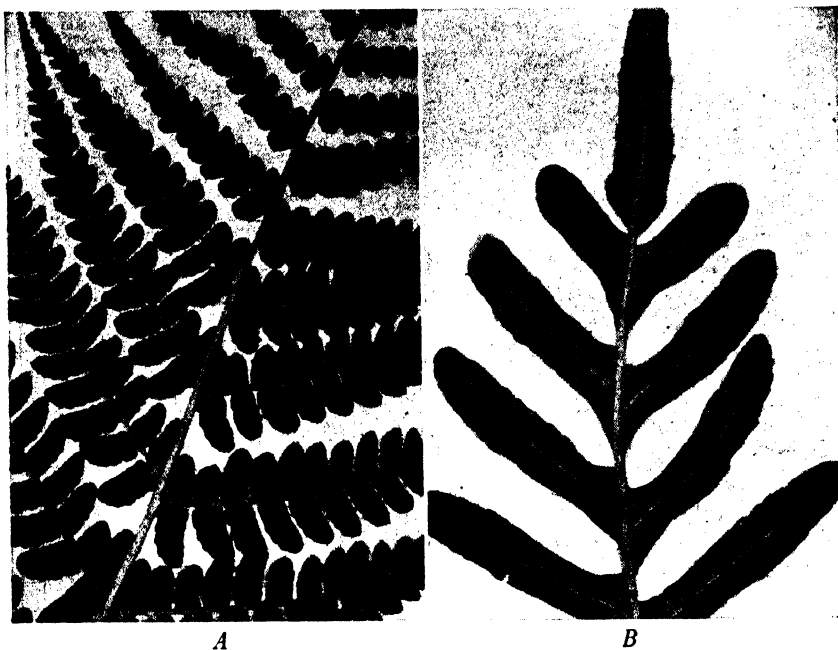
Fig. 251. Arrangement of sori on lower leaf surfaces of ferns

Fig. 253. Section of fern leaf margin, showing
several sporangia.
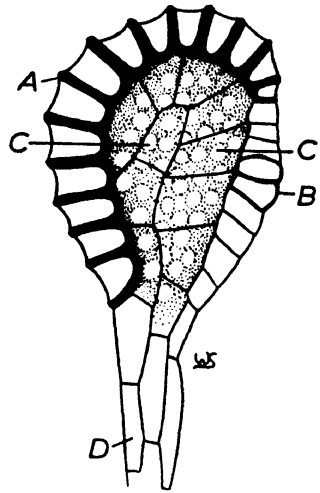
Fig. 254. Fern sporangium

A. Annulus. C. Spores.
B. Lip cells. D. Stalk.

Fig. 255. Fern pro-
thallia growing on a
flower pot.
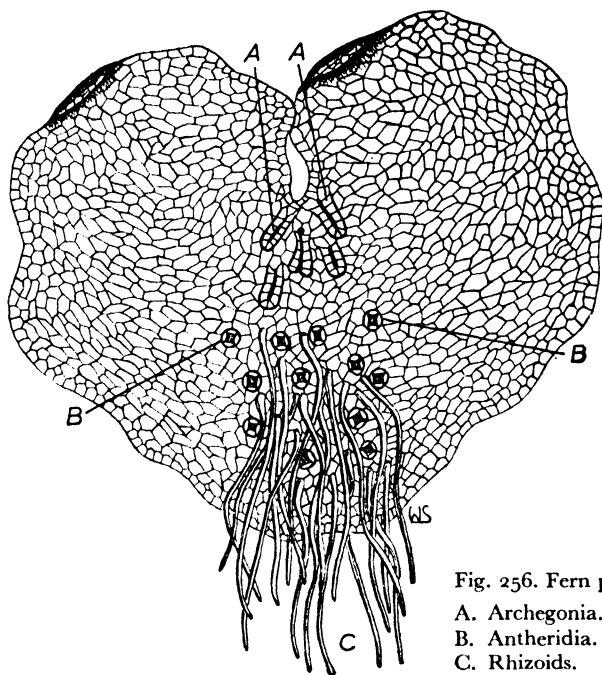
Fig. 256. Fern prothallus
A. Archegonia.
B. Antheridia.
C. Rhizoids.

latter group.. An antheridium produces numerous ciliated sperms, an archegonium a single egg. When a film of water is present between the under-surface of a prothallus and the soil, sperms leave mature antheridia and swim toward the archegonia, usually attracted by certain organic acids secreted by the archegonia. As in the bryophytes, several sperms may enter an archegonium, but only one fuses with the egg. The zygote, like the zygote of a bryophyte, is diploid, as a result of the fusion of haploid gametes, and is therefore the beginning of the sporophyte generation. The zygote is retained within the archegonium and by cell divisions forms a young sporophyte, which derives nourishment from the prothallus for a short time, until it produces its first leaves and roots (Figure 257). It then begins to manufacture its own food, and the gametophyte withers and dies. This young sporophyte ultimately becomes the mature fern plant, which is thus the principal part of the sporophyte generation.

In a few ferns there is a differentiation of leaves or leaflets into spore-bearing and vegetative kinds, but in most species, the same leaves function for both reproductive and vegetative activity.

The ferns are chiefly plants of moist, shaded places. A few species are adapted to dry habitats and are found on dry cliffs in the Southwestern and Eastern United States and other semi-arid regions. A few of them, the water-ferns, are rooted in the mud at the bottoms of shallow ponds or float on the surface of water.

The modern ferns are of relatively little importance to man, except as ornamental cultivated plants. The leaves of bracken ferns are sometimes used as a packing material for fresh fruits and vegetables. The leaves of some ferns produce soft, epidermal hairs employed in considerable quantities as stuffing for pillows and upholstery. The trunks of some of the tree ferns are used for construction purposes in the tropics. The young leaves of some ferns are occasionally used as food by Japanese. A fern, known as male-fern, contains a resin used as a vermifuge.

The ferns and fern allies of past ages formed most of the coal which we use as fuel at the present time. Thus our indebtedness to pteridophytes goes back through the ages to the time when large pteridophyte forests covered most of the earth's land areas and suffered decay and compression which led to the formation of coal. A careful

Fig. 257. Fern prothallus with young sporophyte

A. Prothallus: a. rhizoids.
B. Root of sporophyte.
C. Leaf of sporophyte.

study of certain kinds of coals reveals many fossils of pteridophytes — fossilized leaf fragments, stem pieces, and even sporangia and spores of ferns, horsetails, club-mosses, and their relatives. The study of these fossilized, carbon remains has thrown considerable light upon the vegetation of the Carboniferous Age, during which the great coal beds developed.

2. THE HORSETAILS (EQUISETINAE)

There are about 25 living species of **horsetails,** or scouring rushes, as they are sometimes called. All these species are members of the genus *Equisetum.* In past ages the extinct horsetails were trees which frequently attained heights of 40 feet. At present, however, the remnants of this once-large, vanishing group are slender, cane-like plants which seldom become more than 6 or 7 feet tall. The plants of one South American vine-like species under conditions of abundant moisture reach heights of almost 40 feet. Horsetails grow commonly on river banks, at the edges of ponds and lakes, and frequently in wet ditches or along railroad embankments.

Fig. 258. Reproductive stems of a horsetail (*Equisetum prealtum*)

A. Immature cone.
B. Mature cone, showing individual sporophylls.
C. Scale leaves.

The leaves of horsetails are reduced to small scales. The jointed stems, which are branched or unbranched, are green and are thus capable of photosynthetic activity. They are impregnated with considerable quantities of silica and, as a result, are very rough and harsh in texture. The sporangia are borne in cone-like structures at the tips of the stems (Figure 258). The spores produce small green gametophytes on the soil. The details of reproduction are similar to those of ferns. A "horsetail plant" is the sporophyte generation, just as is a "fern plant."

The horsetails are of little economic importance at present. Their dried stems are occasionally used as scouring materials. As stated above, the tree-horsetails of the Coal Age contributed to the formation of coal.

3. THE CLUB-MOSSES (LYCOPODINAE)

These pteridophytes, like the horsetails, are but a small remnant of what was in the Coal Age a large group of herbaceous plants and trees which often attained a height of 120 feet. The living club-mosses are creeping herbaceous plants which send up more or less erect branches commonly from an inch to a foot tall (Figure 259). They have true roots, stems, and leaves, with well-developed vascular tissues. In the club-mosses, the sporangia are borne on leaves at the apices of the stems. The name "club-moss" is derived from the club-like appearance of the apical cones formed by these spore-bearing leaves (Figures 260, 261). In addition to these, there are other leaves which do not produce spores and which function chiefly as food-making organs. The leaves of club-mosses are usually small and scale-like in appearance, resembling somewhat those of true mosses.

Fig. 259. Club-moss plant (*Lycopodium*)

A. Reproductive branch.
B. Cones (strobili).
C. Vegetative stems.
D. Roots.

In some species of club-mosses, the spores are not all alike as they are in ferns, but are of two distinct structural types, which produce two kinds of gametophytes: male gametophytes which produce only antheridia, and female gametophytes which form only archegonia. As in other plants, the antheridia produce sperms, the archegonia, eggs. The sperms swim through water to the archegonia and fertilize the eggs therein. The zygotes grow into the sporophytes or mature club-moss plants. In some club-mosses, the spores remain inside the sporangium and grow into gametophytes within the sporangial wall. A female gametophyte, thus enclosed by a sporangium, is similar to an embryo sac in the ovule of a flowering plant, for the greater part of an ovule is a sporangium and the embryo sac is actually a female gametophyte. As in an ovule, the young sporophytes of these club-mosses grow in the female gametophytes, inside the sporangia in which the latter developed. Thus, a club-moss sporangium enclosing a female gameto-
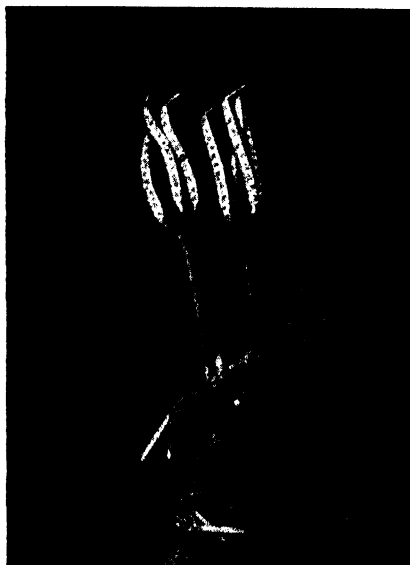
Fig. 260. A club-moss, *Lycopodium com-planatum* var. *flabelliforme*. Note the terminal strobili or cones, bearing sporophylls (spore-producing leaves).

Fig. 261. A club-moss, *Lycopodium obscurum*, showing vegetative leaves, stems, and cones of spore-bearing leaves.

phyte in which a young sporophyte is developing is very similar to a seed, in which the embryo is a young sporophyte growing under similar conditions. In other species, there are only one kind of spore and one kind of gametophyte, which produces both archegonia and antheridia.

The club-mosses (or ground-pines, as some of them are called) grow most commonly in damp, shaded, rich woods. A few species are found in rather dry situations, in rock crevices and on rocky, alpine slopes.

The economic value of living club-mosses is negligible. Some of the evergreen types are used in wreaths and other types of Christmas decorations. A substance known as lycopodium powder, consisting of the spores of species of *Lycopodium*, was used formerly in fireworks and in photographic flashlight powders. Lycopodium powder is also used medicinally in the treatment of certain skin diseases. As mentioned in a preceding section, the club-mosses of the Coal Age were important in the formation of coal. One of the most familiar members of the club-moss group is the resurrection plant (*Selaginella convoluta* and others), which upon desiccation curls into a tight, brownish clump of tissue and upon subsequent wetting quickly unrolls into a beautiful, green plant.

SUMMARY

1. Pteridophytes are land plants with true roots, stems, and leaves.

2. Pteridophytes have a high degree of tissue differentiation, particularly of vascular tissues. Because of their vascular and strengthening tissues, pteridophytes have been able to live more successfully on land and to attain greater size than bryophytes.

3. Alternation of generations occurs in all groups of pteridophytes. The sporophyte generation is always larger and morphologically more complex than the gametophyte generation. As in bryophytes, the sporophyte generation begins with a zygote, the gametophyte with a spore. Reduction division occurs during spore-formation.

4. Both generations are green and autotrophic in most pteridophytes. The sporophyte generation depends upon food supplied by the gametophyte for a short time in its early life until it develops its own photosynthetic tissues.

5. Fertilization in pteridophytes, as in bryophytes, is dependent upon liquid water for the swimming of sperms. The zygote develops inside the archegonium, as it does in bryophytes.

6. The pteridophytes constitute a group of plants which are on the decline. The modern forms are less numerous and for the most part smaller in size than their ancestors of past ages.

7. In some pteridophytes there are two kinds of spores and two kinds of gametophytes, male and female. The female gametophyte is retained within the sporangium in some club-mosses, as is also the young sporophyte, a condition similar to that in the seed development of living seed plants.

8. The modern pteridophytes are considered, not as ancestors of seed plants, but as a closely related group of common ancestry which has evolved to some extent in the same direction as seed plants.

The Spermatophytes: Angiosperms and Gymnosperms

THE SPERMATOPHYTES, or seed plants, of which there are about 195,000 species, outnumber the three other divisions of plants combined. The seed plants constitute the dominant part of the earth's vegetation and are, of all plants, most important to man from the economic standpoint. They furnish the principal necessities and luxuries of human civilization — foods, lumber, textile fibers, cordage, oils, gums, resins, rubber, spices, perfumes, rubber and other latex products, drugs, beverages, cork, dyes, tanning materials, waxes, paper, artificial silk, and other cellulose products. Because of their great importance to man, the seed plants have exerted far-reaching influences upon his history and his culture. Wars have been fought, won, and lost in the struggle for plant power, and migrations of whole peoples have followed the impoverishment of the soil or the knowledge that more valuable plant products could be produced or cultivated in new regions. Many of the world's social, economic, and political difficulties have developed from the struggle for plant resources. The traffic in opium, marijuana, cocaine, and other narcotics, the development of slavery in our country in relation to the cultivation of cotton, the cries of modern dictators for "Lebensraum," the extensive erosion of soils following the cutting away of valuable forests are examples of such difficulties arising from the exploitation of economically valuable plant products. It is beyond the scope of this book to include more than a mention of such strategic crops — rubber, wheat, cinchona (or the "quinine" tree), potato, spices, and many others. The discovery of America was a result, in part, of the desire of European nations to reach the spices and other rich, coveted plant products of the Orient.

The spermatophytes are structurally the most complex and most varied of all plants. They vary in size from tiny, floating duckweeds,

scarcely $\frac{1}{8}$ of an inch in diameter, to the Big Trees of California which are often 30 or more feet in diameter at the base and 370 feet tall. They possess highly developed fibro-vascular tissues and, in most cases, their bodies are differentiated into roots, stems, leaves, and flowers, or cones.

The two most characteristic features of seed plants which set them apart from other living plants are their *production of seeds and their formation of pollen tubes*. These two developments in the seed plants have been largely responsible for their great success as land plants and have doubtless contributed largely to their triumph over bryophytes and pteridophytes as the earth's dominant type of vegetation. Pollen tubes carry the sperms of seed plants directly to the eggs which they fertilize. Thus, fertilization is no longer dependent upon water as it is in bryophytes, pteridophytes and most thallophytes. Pollen tubes have made the seed plants independent of water as a prerequisite to fertilization, and thus seed plants are able to reproduce in locations and under conditions which would render fertilization impossible in the members of the lower plant divisions. Seeds have also been important in enabling seed plants to meet successfully the exacting demands of a terrestrial environment. Seeds contain abundant food for the nourishment of their embryos, they possess coats which protect their embryos from desiccation, from the entry of parasites, from mechanical injury, and, in those seeds with very thick coats, probably from dangerously low or high temperatures. The physiological activities of dormant seeds proceed at an exceedingly low ebb and as a result most kinds of seeds are able to retain their vitality for at least $1\frac{1}{2}$ to 2 years, frequently as long as 10 to 20 years, and rarely for over 100 years. Seeds are efficient reproductive structures also because they, or the fruits within which they develop, are often provided with special mechanisms or modes of behavior which facilitate their dispersal over wide areas.

It should be emphasized again that seeds are not new structures found exclusively in modern spermatophytes. Many extinct plants, the so-called seed ferns, formed reproductive structures scarcely distinguishable from the seeds of modern spermatophytes. In some of the present-day pteridophytes, the club-mosses, for example, the young sporophytes are enclosed and nourished for a brief time by the tissues of the gametophyte generation in a manner strikingly like the development of the seeds of angiosperms and gymnosperms. It seems that nature has tried out a seed-plan in various closely-related groups of

plants, a plan which has reached its culmination in the seeds of sperma-
tophytes.

Another important difference between seed plants and the lower
plant divisions is that the gametophytes of seed plants are much re-
duced in size and complexity and are devoid of chlorophyll, as a result
of which they are completely parasitic on the sporophyte generation
for their nutrition.

A further difference between spermatophytes and the other plant
divisions is the fact that the gametophytes of seed plants are always
of two distinct morphological types — male gametophytes and female
gametophytes. In other plant divisions (except in a few species), there
is only one kind of gametophyte which produces both male and fe-
male sex organs and gametes.

Another feature of most seed plants is the high degree of specializa-
tion among their reproductive organs. In most pteridophytes, the same
leaves carry on vegetative processes and produce spores; in but a few
pteridophytes is there a differentiation into vegetative and reproductive
leaves. In seed plants, the vegetative leaves are ordinarily incapable
of reproductive activity. There are specialized organs some of which
are involved directly, others indirectly, in reproductive processes.
These organs are borne on specialized reproductive branches. In most
gymnosperms, a reproductive branch with its reproductive organs is
called a **cone.** In angiosperms a reproductive branch with its organs
is termed a **flower.** A flower is thus basically similar, from the stand-
point of its developmental morphology, to a cone. Flowers generally
have become more highly specialized than cones, as is apparent in
their greater variability, their numerous specialized pollinating devices,
and in their usual possession of sterile floral organs, namely, sepals
and petals.

1. GYMNOSPERMS

Living gymnosperms number only 630 species. They are all woody
plants, some of them small shrubs, others of them among the largest
living plants. At an earlier time in the earth's development there were
many more kinds of gymnosperms than there are at the present time.
Many of these old, now-extinct species are known to us through the
fossils which they have left in rock strata. Many of these long-extinct
gymnosperms resembled ferns, from which they apparently evolved.

The word gymnosperm means "naked seed," a term descriptive
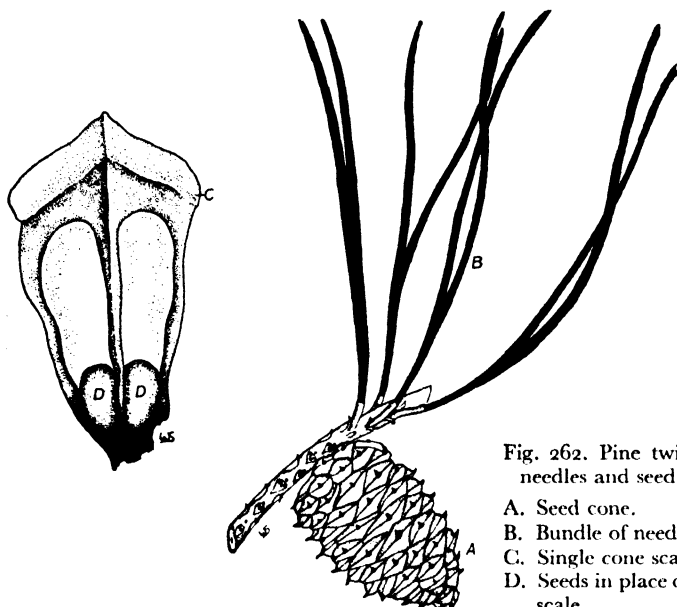
Fig. 262. Pine twig with
needles and seed cone

A. Seed cone.
B. Bundle of needles.
C. Single cone scale.
D. Seeds in place on cone
scale.
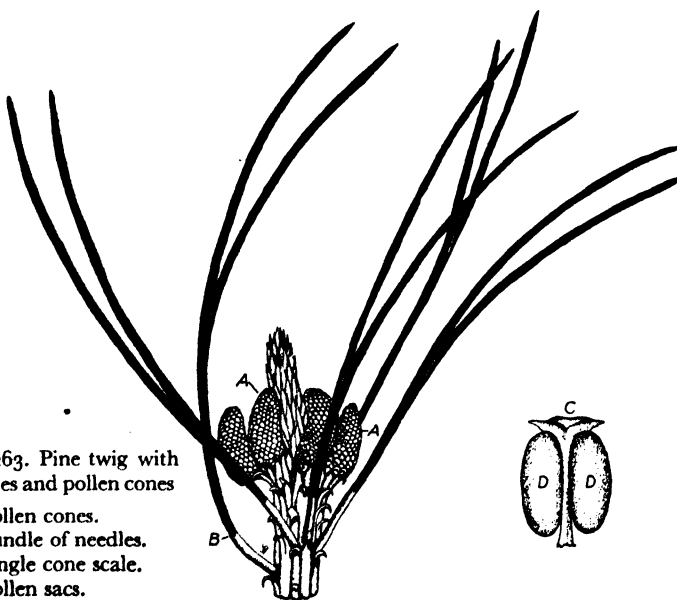
Fig. 263. Pine twig with
needles and pollen cones

A. Pollen cones.
B. Bundle of needles.
C. Single cone scale.
D. Pollen sacs.

of the fact that the seeds of these plants are not formed within a fruit, as are the seeds of angiosperms, but are developed in more or less exposed positions on the surfaces of cone scales (specialized reproductive organs). This is the chief difference between gymnosperms and angiosperms.

In gymnosperms, the trees or shrubs as we see them with the naked eye, are sporophytes. The sporophytes (pine trees, for example) bear cones of two kinds; some cones bear scales (reproductive organs) which produce ovules, others bear scales which form pollen grains. The ovule-producing cones (Figure 262) are usually larger and more woody than the pollen-producing cones (Figure 263). In most gymnosperms, both kinds of cones are borne on the

Fig. 264. Longitudinal section of a pine pollen cone, showing cone scales (stamens) with their pollen sacs containing pollen grains.

same tree, in other species on separate trees. The scales of pollen-producing cones (Figure 264) form pollen grains, those of the ovule-producing cones, ovules.

In the reproduction of gymnosperms such as pines, pollen is liberated from the stamens and is carried by wind to the ovule-producing cones. Pollination in the gymnosperms is entirely by means of wind (Figure 265). The pollen grains sift among the scales of the ovulate cones until they reach the surfaces of the ovules. Some of the pollen grains alight near a tiny pore (the **micropyle**) usually at the top of each ovule. Inside an ovule is a mass of tissue (the female gametophyte) which contains egg cells. In some gymnosperms, several pollen grains near a micropyle form pollen tubes which enter an ovule through its micropyle. In other gymnosperms, the pollen grains lodge in a tiny droplet of liquid which is exuded from the interior of the ovule through the micropyle. As this droplet evaporates, the pollen grains are drawn through the. micropyle into the interior of the seed where they form short pollen tubes which reach the archegonia within which the eggs

Fig. 265. Pine tree shedding pollen. The tree is being shaken to scatter a sufficient amount of pollen to be photographed.

are borne. These pollen tubes (male gametophytes) carry sperms which fertilize the eggs inside the ovule. One or more of these zygotes begin to develop into young embryos. Sometimes mature gymnosperm seeds contain several embryos, more frequently, however, only one full-grown embryo. The fertilized ovules develop into mature seeds, enlarging considerably as they do so, as the result of the passage of food into their tissues.

A seed of a gymnosperm, like that of most angiosperms, contains at maturity an embryo, endosperm (food storage) tissue, and a protective seed coat (Figure 266). The endosperm tissue in gymnosperm seeds develops directly from the female gametophyte and is thus haploid, a condition very different from that in angiosperms in which the endosperm tissue is the product of triple nuclear fusion and is thus triploid (with three times the chromosome number of a gamete). Most gymnosperms mature a crop of seeds in a single season, but some, such as pines, require two full seasons to form their seeds.

Most of the modern gymnosperms are classified into three main groups: **ginkgos, cycads,** and **conifers.** The ginkgos are represented by a single species, a native of the Orient, known commonly as maidenhair tree (Figure 267). It is a handsome tree, which is widely planted in various parts of the world as an ornamental tree. The cycads (Figures 268, 269) constitute a small group of less than ninety species, all natives of the tropics and subtropics. These plants, which resemble small palm trees, are economically important only as ornamental trees in the warm parts of the world.

The conifers (conifer means "cone-bearing") constitute the largest group of gymnosperms with over 500 species. These plants, which have chiefly needle- or scale-like evergreen leaves, are widely distributed on the earth's surface, some of them in the tropics, others in the warmer and cooler portions of the temperate zones. They include a number of well-known kinds of plants, among which are the firs, pines, spruces, bald cypresses, hemlocks, cedars, redwoods, Douglas fir, yews, arborvitaes, all chiefly temperate-zone plants, and the araucarias (or monkey-puzzle trees) which grow in tropical and subtropical climates.

Fig. 266. Longitudinal section of pine seed
A. Seed coat. C. Hypocotyl.
B. Endosperm. D. Cotyledons.

The conifers are exceedingly important to man, especially for the fine softwoods which they produce. The softwoods (conifer woods) have furnished about 80 percent of all of the wood which has been cut in the United States. These softwoods are used directly for construction and many other purposes and also for the manufacture of various cellulose materials, among the more important of which are paper, rayon, cellophane, plastics, and numerous other products. Some of the conifers — balsam firs and pines, for example — furnish resins which are

Fig. 267. Ginkgo twigs

A. Cluster of mature seeds.
B. Twig with leaves and young ovules.
C. Twig with leaves and pollen cones.

Fig. 268. A cycad with ovulate cones (*Encephalartos caffer*).

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Fig. 269. Group of cycads and ferns.

used in the production of turpentine, rosin, tars, and various oils, and in the preparation of cough syrups and other medicines. Several of the pines bear seeds which are highly nutritious and possess good flavors and which are therefore used as human food — among the species which produce edible pine "nuts" is the piñon pine of the Southwestern United States. Hemlocks contain in their bark large amounts of tannins which are used chiefly in the tanning of leather. The "berries" of junipers are sources of aromatic oils used in the flavoring of gin and other alcoholic beverages. Another important use of conifers is their utilization as handsome ornamental trees and shrubs.

2. ANGIOSPERMS

A complete description of the structure and reproduction in angiosperms has been presented in the chapters of Part II of this book. Students should review Chapter XVI on flower structure and functions, at this point, in order to understand the discussion of alternation of generations in angiosperms.

It was emphasized in that chapter that a flower, like a cone, is a

specialized reproductive branch and that its sepals, petals, stamens, and carpels are specialized organs, directly or indirectly concerned with reproduction. An angiosperm plant body, such as a maple tree or a corn plant, is the sporophyte generation of its species. The roots, stems, leaves, receptacles, and floral organs are sporophytic and thus contain the diploid chromosome number in their cells. Of the various floral organs, the stamens and carpels are directly concerned with reproduction. These organs, like the leaves of ferns, bear sporangia. The sporangia of angiosperms are of two types: those which produce **microspores** and those which produce **megaspores.** The sporangia of the first type are borne in the anthers of the stamens, usually 4 in each anther. In these sporangia are formed, following reduction divisions, the microspores which develop into the male gametophytes. These spores are the young pollen grains; the male gametophytes are the mature pollen grains and the pollen tubes which they produce. The sporangia which produce the megaspores are borne on the carpels, inside the ovaries of flowers. Each ovule contains a sporangium, within which 4 megaspores are formed as a result of reduction divisions. Only one of these grows, developing into the female gametophyte, or embryo sac.

The male and female gametophytes of seed plants are thus respectively the pollen grain, with its tube, and the mature embryo sac. These lack chlorophyll, as do the gametophytes of gymnosperms, and are thus completely dependent for their food upon the sporophytes within which they develop. The gametophyte generation begins with a spore and ends at the time of the fusion of a sperm with an egg in the embryo sac. Only the spores, the pollen tubes, the embryo sac, and the gametes are haploid. All other parts of angiosperm bodies are diploid and are thus sporophytic in nature.

The angiosperms are subdivided into **monocotyledons** and **dicotyledons.** The former have flowers with their parts in threes, have a single cotyledon in their seeds, and usually have parallel-veined leaves. The latter have their flower parts in 2's, 4's, or 5's, rarely 3's, have netted-veined leaves, and usually 2 cotyledons in their seeds. There are 45 families and about 40,000 species of monocotyledons, and 258 families of dicotyledons with approximately 155,000 species. The monocotyledons include the cattails, grasses, sedges, palms, lilies, irises, narcissi, tulips, hyacinths, amaryllises, orchids, bananas, and cannas. The dicotyledons include such broad-leaf trees as elms, oaks, hickories, willows, maples, apples, cherries, catalpas, and birches, and also many

herbaceous plants, such as beans, peas, petunias, peonies, columbines, sunflowers, phlox, snapdragons, mints, violets, milkweeds, and many others.

3. SUMMARY

1. The characteristic reproductive structures of spermatophytes are seeds.

2. Seed plants are independent of water for their fertilization since their usually non-ciliated sperms are carried to their eggs by means of pollination and of pollen tubes.

3. The sporophyte generation of seed plants is the dominant generation. The gametophytes, of which there are two kinds, male and female, are much reduced in size, lack chlorophyll, and are dependent for their food upon the sporophytes which produce them.

4. Flowers and cones are morphologically similar; each is a specialized branch, bearing organs involved directly or indirectly in reproductive activity.

5. The principal differences between angiosperms and gymnosperms are:

Gymnosperms	*Angiosperms*
a. The seeds of gymnosperms are borne on the surfaces of cone-scales.	a. The seeds of angiosperms are developed within carpels. A matured carpel-base (ovary) is termed a fruit. Seeds are enclosed by fruits.
b. Gymnosperms are all woody, chiefly evergreen plants.	b. Angiosperms are both woody and herbaceous; many species are evergreen, many are deciduous.
c. In most gymnosperms, pollen grains alight directly upon the surfaces of ovules. The pollen tubes penetrate the ovules directly.	c. In angiosperms pollen grains do not alight directly upon ovules, but are deposited on stigmas. The pollen tubes must grow through the style to the ovary cavity before they reach the ovules.
d. Most gymnosperms have cones, which bear only reproductive organs.	d. Angiosperms have flowers which bear reproductive organs, and usually, in addition, petals and sepals.

Gymnosperms	*Angiosperms*
e. The endosperm tissue of gymnosperm seeds is a part of the female gametophyte and is thus haploid.	e. The endosperm tissue of angiosperm seeds develops as a result of the fusion of a sperm with 2 polar nuclei of the embryo sac and is thus triploid.

6. Both gymnosperms and angiosperms are believed to have evolved from fern-like ancestors which are now extinct.

The Distribution of Plants in Time and Space

The Distribution of Plants in Time: Plant Evolution

1. THE NATURE AND FORMATION OF FOSSILS

WHEN PLANTS die, their bodies are ordinarily decomposed by bacteria, higher fungi, insects, and other organisms of destruction. As a result of this disintegration, the complex organic substances which constitute plant bodies are broken down into simple substances which return to the air and soil and which are then used by succeeding generations of plants in growth and reproduction. These destructive forces usually result in the eradication of all traces of dead plant bodies.

Sometimes, however, decomposition proceeds under conditions which retard the activity of decay organisms and allow changes to occur which result in the preservation of portions of plant bodies. These preserved parts of plants are called **fossils** (Figures 270–277) and are of three types:

1. **Petrifactions,** which are formed as a result of the slow replacement or the embedding of plant structures by rock materials, such as silica, precipitated out of the soil water surrounding and permeating the plant tissues.

2. **Impressions,** which result from the burial of plant parts in soils which subsequently harden into rock, in much the same manner as an imprint is left when a leaf is pressed into the surface of wet cement which is then allowed to "set." Impressions thus preserve the external structural features of plant parts.

3. **Original substances,** that is, some of the original material which composed the plant body, are preserved, usually in the form of carbon, as, for example, in coal.

The process of petrification usually preserves very accurately the details of both internal and external structure, each cell being replaced by rock materials retaining the form and size of the original cell. For
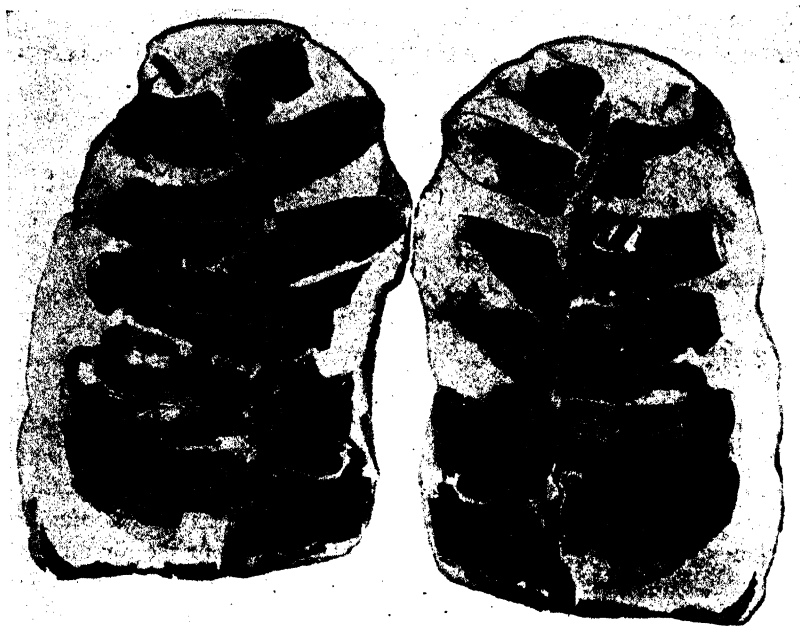
Fig. 270. Fossilized leaf of a fern, *Neuropteris flexuosa*.

Fig. 271. Portion of a fossilized stem of *Lepidodendron*, a Carboniferous tree club-moss.
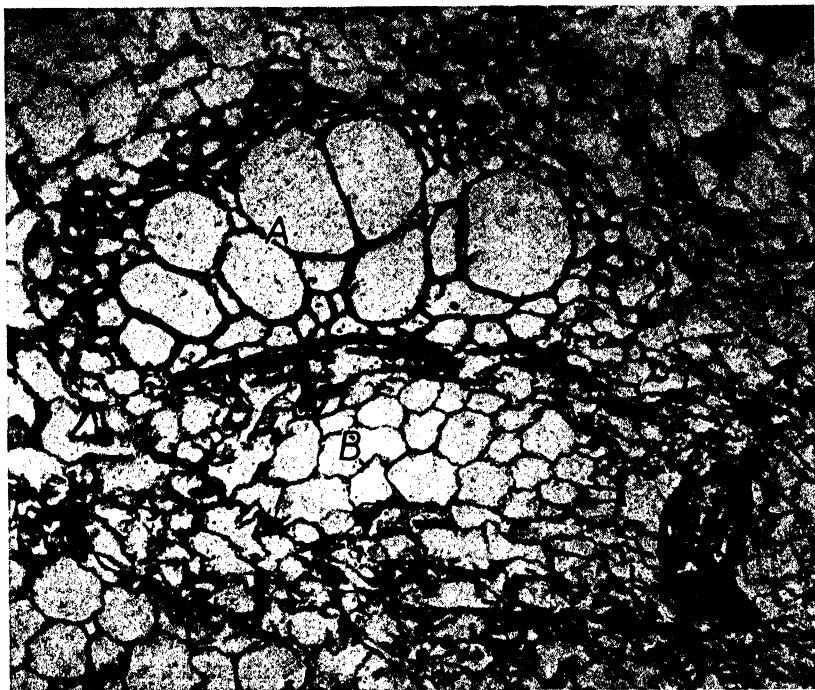
Fig. 272. Cross-section of the vascular bundle of a fossilized petiole of *Myeloxylon*.
A. Xylem, B. Phloem.

this reason, the study of petrifactions is generally more revealing than the study of impressions and original substances. Fossils of the latter types are more common, however, and despite their usual lack of minute structural detail, they have given botanists much information concerning the plant life of the past.

The study of plant fossils (*paleobotany*) shows that different kinds of fossils occur in the various layers of rock which constitute the earth's crust, an observation which leads to the conclusion that the earth's vegetation has not been constant and unchanging, but that different types of plants have inhabited the earth's surface at different periods during its history. Paleobotanical investigations have demonstrated that the kinds of fossils found in each rock stratum are generally not sharply distinguished from fossils found in other strata, but that structural similarities can frequently be traced from the fossils of one layer to those of other layers formed before and later. The presence of such

Fig. 273. Longitudinal section of a portion of a fossilized *Psaronius* root. Notice the sculpturings of the xylem cell walls and the large tyloses.

morphological resemblances in plants of different geologic ages indicates that close relationship exists among them and that the plants of various periods have developed from plants of earlier times. The changes which have appeared in the earth's vegetation in successive geological periods are believed to have occurred partly as a result of gradual alterations in the earth's climatic and topographic features. A study of the many kinds of plant fossils which have been discovered by paleobotanists shows that there has been an increasing complexity in the structure of many plants from the fossils of the oldest rock layers to the plants of the present time. An interesting feature of the many types of plant fossils found in the earth's crust is their characteristic appearance in certain strata of rock; geologists commonly recognize and classify various kinds of sedimentary rock by the nature of the fossils found in them.

Among the numerous perplexing and biologically significant questions which arise from a study of the vast panorama of plant transformations in the earth's history are the following: What was the nature of the first living plants, whence did they come, what kinds of plants appeared during each geological age, what evidences of relationships are discernible among them, what factors produced the alterations which plants have undergone, what were the probable ancestors of our modern living plants? The remainder of this chapter presents the consensus of modern botanical investigationsb earing upon these questions.
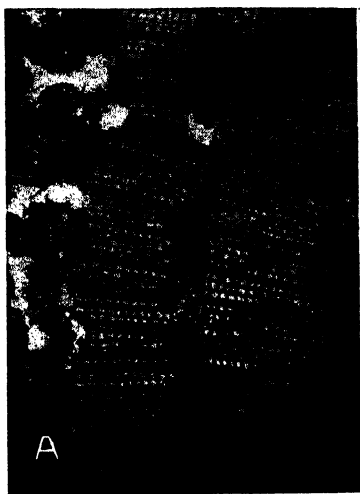
Fig. 274. Silicified fossil wood of *Dadoxylon*
A. Transverse section, showing tracheids.
B. Radial section, showing pits in tracheid walls.

Fig. 275. A fossilized spore of *Triletes* from a Southern Illinois coal ball. 45x.

Photo by J. M. Schopf, Illinois State Geological Survey

Fig. 276. Two fossilized spores of *Mazocarpon*.

2. THE FIRST LIVING PLANTS

As indicated in Chapter II, the origin of the first life on earth has never been explained. Although the problem of life's beginning upon our planet interests every biologist, it remains a subject for speculation, about which, so far, only indirect evidence has been obtained. It is possible, though remotely so, that some biologist of the future may discover living protoplasm arising from non-living materials, but even such a tremendous discovery as this could not reasonably be offered in explanation of an event hidden irretrievably in the mists of the earth's antiquity. Thus, for the present we can but speculate upon the possible nature of the first living plants and the conditions involved in their origins.

Since the earliest recognizable plant fossils are those of morphologically simple algae and bacteria and since the fossils from later periods in the earth's history give ample evidence of steadily increasing structural complexity, it seems reasonable to suppose that the earliest plants were at least as simple in their structures as the most primitive thallophytes, if not simpler. The bodies of simply organized algae

Photo by J. M. Schopf, Illinois State Geological Survey

Fig. 277. Longitudinal section through a fossilized cone of *Mazocarpon*, showing sporangia and growing point. 12x.

and bacteria are so soft and delicate that they decompose rapidly after death and thus do not ordinarily leave fossil impressions or petrifactions. Thus, fossil records of such organisms are rare and no unmistakable evidence concerning the first living plants has been derived from the record of the rocks.

Biologists agree that the first living organisms of the earth must have been plants, for only plants could, with the aid of solar or chemical energy, convert minerals and simple atmospheric gases into living protoplasm. This ability is found in no known animal. It is believed that these pioneer plants must have originated in the waters of the

earth, for all of the early plant fossils are apparently those of aquatic plants, with structural features unsuited to land environments.

Many botanists think that these first plants were bacteria, perhaps identical with some of those now living or at least similar to them. In some of the oldest rock strata of the earth's crust are found deposits of limestone, graphite, and iron, substances which are known to be formed in part through the activity of primitive thallophytes. There are bacteria still actively engaged in building up such deposits in our present-day world. One of these organisms is *Leptothrix*, the iron bacterium, which causes iron-charged waters to deposit their burden in the form of yellowish-rusty blobs of iron-oxides. *Leptothrix* has apparently carried on its iron-precipitating activity through many eons of earth history, for fossils of it have been found in very ancient layers of rock. From its oxidation of iron compounds, *Leptothrix* derives the energy which it uses in manufacturing organic substances from inorganic materials, a synthetic process independent of light, requiring the presence only of iron and of raw materials to work upon. The tremendous Mesabi iron seam of the Lake Superior region is believed to be largely a product of *Leptothrix* activity. Similar to *Leptothrix* in their independence of light as a source of energy and in their ability to synthesize organic substances from inorganic with the aid of chemical energy are other autotrophic bacteria. One of these, *Beggiatoa*, derives its energy from the oxidation of hydrogen sulphide, another, *Cladothrix*, is powered by the oxidation of manganese, still others of these autotrophic bacteria live by the controlled combustion of nitrogenous materials, hydrogen, marsh gas, and other substances.

The discovery of fossil remains of certain of these chemosynthetic bacteria, the tremendous deposits of iron, of limestone, and graphite formed at least in part through bacterial action, the aquatic nature of these bacteria, their ability to live independently of light, a factor of great importance in what was doubtless a misty, dim world, and their utilization of the energy of chemical oxidations for organic syntheses, a method far simpler than the elaborate chemistry of photosynthesis, lend weight to the speculation that the earth's first plants may have been built upon such relatively simple architecture as that of the chemosynthetic bacteria.

The next phase in the development of the earth's vegetation may have been the appearance of chlorophyllous plants, able to manufacture organic materials only through the process of photosynthesis in 'the presence of light. The earliest of these green plants were probably algae,

the oldest green plants in the fossil record and morphologically the simplest of modern green plants. The blue-green algae may have been among the first algae to appear, for fossils of what seem to be blue-green algae have been found in ancient rocks. Further, blue-green algae are very similar to many bacteria in their structural organization and many of their physiological activities. Like bacteria, they have a relatively undifferentiated type of protoplasm without nuclei and plastids, and they reproduce entirely by asexual methods, as do the bacteria. Coincident with, or following the appearance of blue-green algae, there may have developed primitive types of animals, probably microscopic and unicellular, like the bacteria and blue-green algae themselves, and later, other more complex types of algae.

The appearance of green plants was the beginning of a great forward movement in the plant world, for it established a mode of nutrition which was to become dominant among plants and it initiated lines of development destined to lead through the ages to the infinitely varied floras of modern times.

3. THE GEOLOGICAL RECORD

Since the time when the earth was first formed, continuous changes have taken place in its surface. As soon as water and the atmosphere appeared, decomposition and disintegration of the rocks began. These processes, called **weathering,** together with the grinding, scraping, and transporting action of winds, water and ice, slowly eroded the land and deposited the resulting sand, clay, and lime in the shallow seas bordering the continents. Less extensive deposits of these sediments also developed in lakes, swamps, and the flood plains of rivers. All these deposits, consisting of horizontal layers, or **strata,** may include the buried remains of plants which either grew in the deposits or were washed into them. Ultimately, through long periods of time, the sediments hardened to form **sedimentary** rocks and the engulfed plants became fossils. Later, as a result of slow, crustal uplift, some of these rocks became dry land and the fossils which had their origin in a swamp or sea often appear in a hillside or even at the summit of a mountain. The processes of weathering, erosion, sedimentation, and uplift have occurred through many geologic periods and of course are still going on at the present time.

The various sedimentary rock strata which form a major portion of the earth's crust have been deposited in the order of the time of their

formation, with more recently formed layers deposited upon successively older ones. Thus, the oldest rock strata are those now found at the bottom of any given sequence of layers and the more recently formed ones occur above these in order. Geologists have been able to estimate in a rather general fashion the age of the earth and the ages of the various rock strata. Such estimates are based upon various kinds of evidence. The rates of accumulation of salt in the sea and of the decomposition of radioactive substances, such as uranium and thorium are the best measures of the total length of geological time. Smaller time divisions are determined approximately by studies of the rates of erosion and of the deposition of sediments. Then, a comparison of the rock layers in different places and of the fossils contained in them enables geologists to piece together a sequence of strata from oldest to youngest. By adding the estimated ages of all the rocks in this chronological series or rock column, geologists arrive at a figure for the total duration of geologic time.

As a result of their studies, geologists have separated the geologic history of the earth into five major time *eras;* these in turn are subdivided into *periods*, and these into smaller time intervals called *epochs*. Generally accepted calculations indicate that the oldest rocks of the earth's crust are nearly two billion years old. Oldest of the geologic eras is the Archeozoic, most recent is the Cenozoic, of which our present time is a portion. The five geological eras and their approximate years of duration are as follows, with the oldest era at the bottom of the list, the most recent at the top, in the same order as the arrangement of their various strata in the crust of the earth:

Eras	*Duration in Millions of Years*
Cenozoic	60
Mesozoic	135
Paleozoic	355
Proterozoic	650
Archeozoic	800
Total	2000 millions of years

The kinds of plants which developed during the eras, their distributions upon the earth, and their survival or extinction have been influenced markedly by climatic changes during these tremendous time intervals. Throughout vast lengths of time, temperature changes appear to have been slight, but within shorter periods of time and somewhat limited areas the earth's climates have varied from moist to dry,

from warm to glacial. It is difficult to characterize each era in terms of climate, for frequently even at the same time differences in climate at different parts of the earth's surface were very great. Our knowledge of past climates of the earth is based largely upon the nature of the plants and animals present, their distribution, their habits of growth, and the presence or absence of annual rings in trees. Thus, information about the climates of the Archeozoic and Proterozoic eras is necessarily meagre; there are some evidences of glaciation in these eras, but apparently there were also periods of exceedingly mild climates. In the early Paleozoic there were extensive glaciations; in the middle and late Paleozoic, the climate over vast areas of the earth was warm, moist and fairly uniform, with brief periods of glaciation and coolness. During the Carboniferous period, the warm, equable, moist climate was especially favorable to a lush vegetation. In the succeeding and final period of the Paleozoic era, however, the earth's climate became generally cooler and more arid than it had been during the Carboniferous period, a transformation which may have been in large part responsible for the extinction of certain Carboniferous plants. The Mesozoic era began with rather cool temperatures and considerable aridity, but later in this era, warm temperatures and considerable precipitation characterized much of the earth's surface. In the late Mesozoic era the climate once more became generally cooler and drier. Through most of the early and middle Cenozoic era temperatures were rather mild and equable and the climate seemed to have been rather generally moist. As the Cenozoic era lengthened, gradual cooling set in and with it, increasing aridity. In the late Cenozoic era came great periods of glaciation and with them marked changes in the earth's vegetation to be described later in the chapter.

The Archeozoic Era. No fossils of plants or animals have been discovered in Archeozoic rocks, which are chiefly igneous (formerly melted) or metamorphic rocks (those hardened and recrystallized by heat, water and tremendous pressures within the earth). Such rocks are found in the ancient Laurentian mountains of Canada and in the innermost gorge of the Grand Canyon. A few sedimentary rocks appeared in the later years of the Archeozoic. It is possible that very primitive types of life may have appeared in the late Archeozoic, but no evidences of their presence have been discovered. The accumulation of graphite in the Archeozoic is considered by some biologists to constitute evidence for the existence of living organisms.

The Proterozoic Era. The sedimentary rocks of this era have yielded

up a few doubtful fossils of primitive plants — possible algae and bacteria. However, extensive deposits of iron, graphite, and carbonates in Proterozoic formations are considered to be in part products of the metabolic activities of primitive plants. Graphite is almost pure carbon and may have accumulated as a result of the activities of plants which fixed the carbon dioxide of the atmosphere in the form of complex organic compounds. The oxides in certain iron ore deposits are believed also to have been precipitated by bacteria similar to or perhaps identical with *Leptothrix*, and Proterozoic limestone (calcium carbonate) beds were possibly secreted by algae, perhaps of the same stock as the limestone-algae of the present day.

The Paleozoic Era. In the rocks of the various periods of the Paleozoic is a succession of numerous and varied types of plant fossils. In the earliest period, many algae thrived, not only those of simple pattern, such as blue-greens and greens, but also more highly differentiated types similar to our modern browns. Many of these algae were species which secreted calcium carbonate and thus built up vast beds of calcareous rocks. In the early Paleozoic, vast warm seas covered much of the earth and constituted a singularly suitable medium for the extensive development of primitive aquatic plants.

Near the middle of the long Paleozoic era there appeared what were probably the first true land plants, the first to leave the relatively simple and easy life of the water and encounter the more difficult and more varied problems of terrestrial environments. These first land plants, known as *Psilophytales* ("naked plants"), are no longer among the earth's living plants but are known to botanists through numerous fossils found in the Paleozoic rocks of Britain, Germany, Gaspé, New England, and Australia. These fossils, found in the rocks of what has sometimes been called the "Age of Seaweeds," have aroused great interest among paleobotanists and are regarded as among the most significant fossils ever discovered, from the standpoint of their bearing upon the knowledge of the evolution of land plants.

The genus *Psilophyton* is appropriately named, for its fossils show it to have been a very naked, wiry kind of herbaceous plant, scarcely a foot high, without leaves or roots, but with sparsely branched stems bearing sporangia at their apices, and underground stems with small rhizoids. Closely related to *Psilophyton* are two other genera, *Rhynia* and *Hornea*, known through fossils fundamentally like those of *Psilophyton*. Some of these psilophytes had small, primitive leaves but even in these plants the stems were the best-developed and most conspicuous parts of the plants.

In their anatomical features, the psilophytes show many resemblances to more recent groups of vascular plants, structural features indicating adaptation to a land habitat and lacking in the aquatic algae. The surfaces of psilophyte bodies were covered by epidermal layers with stomata and the stems had a considerable degree of differentiation of vascular and strengthening tissues. The spores were thick-walled and cuticularized and were in many respects like the spores of modern, living pteridophytes. The epidermal layers doubtless conserved water within the primitive stems and the differentiation of vascular and strengthening tissues facilitated the upward movement of water and dissolved materials from the rhizoids and underground stems, and provided support for the branching thallus-like bodies. The protoplasts of the epidermal cells seem to have secreted cutin onto the outer walls of the cells in much the same manner as do the epidermal cells of modern land-plants. The vascular tissues were only slightly differentiated, but cells of both xylem and phloem were present in the stems together with distinct cortical tissues. Thus, these possibly-first land plants possessed the same fundamental morphological equipment which occurs in our modern land plants and which enables them to obtain and conserve water effectively, to grow erect, and to develop bodies of considerable size. The development by early water plants of such structures represented an important advance and one which made possible the migration of these plants from a water to a land environment, thus apparently establishing an evolutionary trend which has led to the more recent and more diverse land floras.

Botanists are not in complete agreement concerning the probable evolutionary significance of the psilophytes. Some regard them as close relatives of certain kinds of liverworts and as a possible transitional group between bryophytes and pteridophytes. Other botanists consider that the psilophytes show more fundamental similarities with certain of the green algae from which the psilophytes may have evolved.

The latter view, namely, that the psilophytes had their origins among the algae is strengthened by the fact that all of the known bryophyte fossils have been found in rock strata formed later than those in which the psilophytes appear. In other words, the fossils seem to indicate that recognizable bryophytes appeared subsequent to the time of origin of the psilophytes and that thus they could not have been ancestors of the psilophytes. Most botanists now believe that both bryophytes and psilophytes evolved from algae, the psilophytes at a somewhat earlier time than the bryophytes. Though botanists thus

differ in their views concerning the origin of the psilophytes, they agree generally that these plants are distinctly pteridophytous and that more recent groups of pteridophytes have probably evolved from them.

Also in the Paleozoic, plants strikingly similar to our present-day club-mosses, horsetails, and ferns appeared on the stage of nature and formed the dominant vegetation of the earth during most of the later years of the era. There were tree-like club-mosses which reached heights of over 100 feet and formed extensive forests, as well as smaller, herbaceous species which were possibly the ancestors of our living club-mosses. Also among the common plants of the middle and late Paleozoic era were calamites and other horsetail-like plants, which frequently reached heights of 100 feet, with stems nearly 3 feet in diameter. Ferns of numerous types likewise formed an important part of middle- and late-Paleozoic floras; among the more complex ferns of the late Paleozoic were the "seed-ferns," plants which resembled ferns in their general structure and their superficial appearance, but which actually were more closely related to the cycad types of gymnosperms. These "seed-ferns" bore ovules which developed into seeds resembling those of gymnosperms. The Paleozoic club-mosses, calamites, ferns, and seed-ferns constituted the major portion of the vegetation during the Carboniferous period (Figure 278) of the Paleozoic era. The death and partial decay of these Carboniferous pteridophytes led to the formation of extensive coal deposits which are very important in our modern civilization.

Toward the end of the Paleozoic era, these ancient pteridophytes went into a decline which led to the extinction of many species which had flourished in the Carboniferous. Also in the closing years of the Paleozoic there grew extensive forests of gymnosperms, plants more like our living gymnosperms and less similar to ferns. These plants, now extinct, seem to have been the ancestors of more recent groups of gymnosperms.

Thus, the Paleozoic encompassed a series of momentous events in the evolution of plants. What was perhaps the most significant advance in the history of the earth's vegetation occurred in the early Paleozoic — namely, the migration from a water to a land environment, a movement made possible by important changes in the architecture of plants, and in turn favoring further changes which led ultimately to the development of modern seed plants. The Paleozoic era opened with a well-developed aquatic flora of algae and fungi, saw the rise of the first land plants, the psilophytes, and an infinite variety of ferns and

Fig. 278. Restoration of a Carboniferous swamp forest, Field Museum of Natural History. The vegetation consists of giant horsetails, club-mosses, ferns, and primitive conifers.

fern-allies, then closed with the appearance of the seed-habit and of seed plants closely related to our living cycads and conifers.

The Mesozoic Era. In the early Mesozoic era occurred the rapid development and diversification of gymnosperms and the disappearance of most of the seed-ferns and giant horsetails and lycopods of the Paleozoic. Cycads, maiden-hair trees, and conifers formed extensive forests. The early Mesozoic conifers were for the most part unlike our more common present-day types; they were mostly like the living araucarias (monkey-puzzle trees) of Australia and New Zealand. The extensive forests of petrified trees in Arizona and other parts of the Southwestern United States are composed largely of gymnosperm fossils of the araucarian type. As Mesozoic time progressed, other kinds of conifers appeared, among them pines, yews, redwoods and cypresses. During the greater part of the Mesozoic the conifers constituted the dominant vegetation of the earth. They were numerous, not only in individuals, but likewise in species. Fossils show that there were many more kinds of conifers during the closing years of the Mesozoic than there are on the earth today. The gymnosperms reached their zenith then and have since been traveling the road to extinction, a mere remnant of about 640 species having survived through the present time.

The diversification and ascendency of the conifers was the most conspicuous vegetational transformation of the early and middle

Mesozoic. A second equally important historic event occurred during the closing years of the Mesozoic — the appearance of the first true angiosperms, the first "flowering" plants. The ancestry of these earliest angiosperms is unknown; a commonly accepted theory is that they arose from some group of highly specialized seed-ferns, possibly similar to those cycad-like plants from which the gymnosperms took their origin. The dispersal and evolution of the angiosperms during the late years of the Mesozoic was so rapid that by the end of the era they had surpassed the declining conifers as the dominant plants of the earth. As the early angiosperms prospered, so the conifers and pteridophytes faltered and by the beginning of the Cenozoic had become a much-reduced remnant of once-dominant races. The vegetation of the closing years of the Mesozoic era must have had a very modern appearance, for willows, magnolias, tulip-trees, elms, oaks, sassafras, palms, maples and numerous other present-day types of trees formed extensive forests. Fossils of these genera, together with those of many other kinds of angiosperms, have been taken in great numbers from the strata of the late Mesozoic. Thus, the Mesozoic may be regarded as the cradle of our present dominant plant group, the spermatophytes.

The Cenozoic Era. The Cenozoic era has been appropriately labeled "the age of flowering plants," for the angiosperms during this era entrenched themselves as the dominant plants of the earth, while other older groups had traveled farther along the road to extinction. During the Cenozoic the evolution of angiosperms was extensive and remarkably diversified and has resulted in the very rich assortment of flowering plants which now extend over the land from the Arctic circle to the Antarctic. Evolution within the angiosperms is still apparently following a progressive pattern; that is, the diversification of flowering-plant types is still continuing and will doubtless produce an even richer and more varied angiosperm flora in the centuries to come.

In the early part of the Cenozoic era, the angiosperms were chiefly woody plants, such as those which developed toward the close of the Mesozoic. Along with the fossils of those angiosperms mentioned in the preceding section of this chapter, fossils of many other woody angiosperms have been found, both in the Mesozoic and Cenozoic — fossils of birches, sycamores, figs, eucalyptus, persimmons, and many other genera. In strata of the late Mesozoic and of the early Cenozoic, leaf fossils of such herbaceous angiosperms as sedges and possibly thistles have been found, but these fossils are few as compared with the numerous fossils of woody plants. The geological record thus strongly suggests

the dominance of woody angiosperms in the late Mesozoic and in the Cenozoic until comparatively recent times. In the early Cenozoic, the climate was warm over most of the earth and great forests of woody angiosperms covered most of the land; figs, laurels, palms, redwoods and other plants which are now found in the tropics or in areas with the milder middle latitude climates, flourished in northern Europe and North America, and even grew abundantly in Greenland. Such distribution is evidence of the mild climate of far northerly regions in the early Cenozoic. As the Cenozoic era lengthened, the climate became cooler, especially at the poles, and generally drier. Toward the close of the Cenozoic era, about one and one half million years ago, came the Great Ice Age, which resulted in the extinction of many warmth-loving plants growing near the poles and the retreat equatorward of others before the slowly advancing ice sheets. Thus, during these periods of cooling in the middle and late Cenozoic, marked changes in the distribution of the woody angiosperms occurred, changes which resulted chiefly in more restricted ranges of these woody plants. Concomitant with the progressive cooling and drying of the earth came a great increase in the numbers of herbaceous plants. Many botanists believe that this progressive refrigeration and drying were important factors in the rapid evolution of herbaceous plants. Low temperatures of winter in sub-arctic regions, according to this idea, killed most of the trees which were unable to withstand extremely low winter temperatures. Herbaceous plants, however, were able to survive under such conditions, often as annuals, which are able to grow quickly from seeds and produce another generation of seeds within the short summers of sub-arctic regions and which are thus able to live from year to year, not as individuals in vegetative condition but through their seeds which lie dormant during the bitter cold winters and spring into growth and fruition during the next brief summer. More frequently, in these cold areas, the herbaceous plants are perennials, the aerial parts of which are killed by low winter temperature, the underground parts of which, however, are able to survive as a result of protection offered them by their subterranean habitat. It is believed that the first effects of refrigeration upon woody plants of the far north were to stunt and dwarf trees into shrubby plants and thus shorten the time required to attain maturity. Later, with increased refrigeration, the more tender plants were killed off, and the surviving, reduced woody forms became gradually transformed into perennial herbs, which could stand being killed back to the ground every winter, or into an-

nual herbs, which could produce seeds in a single short-growing season. This generally accepted explanation of the phenomenally rapid rise of herbaceous angiosperms is supported by many lines of evidence, one of which is the high percentage (75–93 percent) of herbaceous plants in sub-arctic and higher middle latitudes and the high percentage of woody plants (46–88 percent) in the sub-tropics and tropics. Thus, it may be said that the most recently evolved angiosperm flora is herbaceous, a flora which represents the culmination of plant evolution at the present time.

4. THE NATURE OF EVOLUTION

The word "evolution" embodies the idea of a series of related changes proceeding in an orderly succession; each of these changes may be regarded as a product or resultant of earlier changes and as an ancestor or progenitor of future changes. The idea of evolution thus involves not merely the idea of change but emphasizes as an essential feature the existence of an orderly series of changing events. In this sense, "evolution" is widely used in many fields of human thought and achievement as a designation for numerous and varied related phenomena of transformation and growth. Thus we speak of the "evolution of the aeroplane," the "evolution of the symphony," the "evolution of impressionism in art," the "evolution of the earth," and the "evolution of man." The fundamental implication in all of these statements is the idea of change, of impermanency, and orderly development. Many of the philosophers of Ancient Greece were convinced of the continuous change and flux in many of the entities and phenomena around them and in holding such views were the first spokesmen for the concept of evolution. These unceasing changes, the philosophers observed, were sometimes unpredictable and seemingly haphazard, but more often appeared in regular rhythms or cycles, so that they could frequently be described in advance of their actual occurrence.

If one is observant, he must be impressed by the changes which go on about him in the non-living world. Among these changes is the occurrence of climatic cycles. The weather of the individual seasons varies from year to year, and even within the short span of a human life, one may detect climatic cycles; for example, a series of years, with very cold winters, may be followed by a number of years with warmer winters and several summers of scanty rainfall are again succeeded by summers of heavy precipitation. A study of the annual rings of trees

leads to the conclusion that in a given region climatic cycles are pronounced even within short spans of time. Plant fossils in rock strata give testimony to climatic changes through much longer periods of time and thus add evidence of past climatic cycles.

Topographic transformations are generally slow, but despite the gradual nature of most of these changes, one may see evidences of alterations in the earth's surface — the wearing away of soil by wind and water, the fragmentation of rock by frost-action, the filling of ponds and lakes by wind- and water-borne debris, and the shifting of surface rocks and sediments as a result of forces within the earth. Evidence of topographic changes in the distant past is the presence of fossils of aquatic plants and animals in rock strata now found in high mountain ranges, far above the levels of seas or lakes. Such strata obviously must have lain at some time beneath the surface of water inhabited by plants and animals, and subsequently must have been pushed upward far above present water levels during processes of mountain building, as has been previously stated.

Such changes in climatic and topographic features, together with numerous other chemical and physical transformations both on the earth and on other heavenly bodies, are embodied in the concept of *inorganic evolution*, a concept of fundamental importance in the study of geology, astronomy, chemistry, and physics. Though the concept of evolution has thus established itself as a mode of thought in the physical sciences, it is more familiar to the layman in its application to the development of living organisms, especially of man. The concept of *organic evolution*, or the evolution of plants and animals, has influenced all fields of biological science and is today a point of departure, a working blue-print in many phases of biological investigation. This concept holds that the first living organisms on the earth were very simple in structure, that all plants and animals which have appeared on the earth are descendants of the simple, primordial organisms, and that during the main course of evolutionary change, there has occurred an ever-increasing structural complexity and diversification. In some groups of plants and animals, processes of simplification have occurred, resulting in the evolution of structurally simple organisms from morphologically more complex ancestors. Transformations of this type have appeared as switch tracks along the trunk lines of evolution and thus have not fundamentally altered the major evolutionary tendency toward increased complexity and specialization.

Reputable biologists agree generally upon the fact of evolution.

That living organisms arise from pre-existing plants or animals, that living organisms occasionally produce descendants somewhat different from the parents, and that different kinds of plants and animals have inhabited the earth at different phases of its history are undisputed facts, which have been proved upon numerous occasions by careful observations and by actual experiments.

Explanations other than that offered by the concept of evolution have been proposed to account for the presence of the myriad types of plants and animals which now live or have lived upon the earth. Chief among these alternative suggestions has been the Theory of Special Creation, according to which each kind of plant and animal upon the earth's surface has been created as a separate, distinct, unchanging entity, incapable of giving rise to other kinds of living organisms. The Theory of Special Creation is not accepted as a sound biological principle by most biologists, for the evidence available is wholly opposed to this theory and in favor of the Concept of Evolution. The morphological similarities found in the plants and animals of different periods in the earth's history, the existence of numerous intermediate organisms bridging the gaps between species of one period and those of another, the increasing complexity of structure in both plants and animals through geological history, and the actual, demonstrable, present-day origin of new types of plants and animals from older types, all support the idea that the many kinds of living organisms on the earth have developed from older types of organisms and that they have not been created as fixed, immutable entities. Thus, the Theory of Special Creation has been replaced in biological thought by the Concept of Evolution.

A common popular misunderstanding is that the idea of organic evolution is merely a theory concerning which there is much disagreement and dispute among biologists. Actually most biologists agree that evolution is a fact, proven as definitely and irrefutably as the production of seeds by flowers or the manufacture of glucose in photosynthesis. Whatever disputes occur among biologists concern the *causes* of evolution, the fundamental *reasons* for processes of change in living organisms, not the *facts* of evolution upon which biologists are generally in accord. As knowledge of the facts of evolution expands, biologists will doubtless synthesize their diverse observations and conclusions upon evolutionary changes into a unified explanation of the actual causes and mechanisms of this most fundamental and characteristic biological process.

Thus, modern science offers a dynamic interpretation of the development of the earth and of its inhabitants, an interpretation which rejects the idea of fixity and emphasizes the universal operation of more or less orderly processes of change. The researches of astronomers, geologists and other physical scientists have given us a dynamic story of the origin and evolution of our planet and have shown the fallacy of the old belief that the earth came into existence in exactly the same form and structure which it has today. Similarly the investigations of biologists have drawn a vast panorama of teeming, plastic, ever-changing living beings upon the earth's surface, a panorama which represents a continuous parade of exceedingly varied organisms, all of them with a common, ultimate origin, all of them related in varying degree because of their common descent.

5. THE EVIDENCES FOR EVOLUTION

The evidences which have led most biologists to accept evolution as a demonstrated fact are many and have been derived from studies of many aspects of plant and animal life. The most significant evidences for the fact of evolution have been derived from the study of fossils, from observations upon comparative morphology and development, and from investigations upon physiological activities, inheritance, domestication, geographical distribution, and intergrading species.

Fossil Evidence. Perhaps most impressive of the evidences for evolution is the testimony of fossils, transcribed by the patient work of paleontologists, as described in an earlier section of this chapter. The study of plant fossils demonstrates that different kinds of plants have inhabited the earth during different geologic eras, that many evidences of relationship exist among the characteristic plants of different eras, that the structure of plants has become more complex and more highly specialized through the earth's history, and that many kinds of plants have arisen, lived for a time and then passed on to extinction. The fossil record may be thus regarded as indisputable and concrete evidence of change in the earth's vegetation during geological history.

Morphological Evidence. The study of morphology, or structure, is a source of important evidence for the facts of evolution. Marked structural similarity indicates close relationship, less striking structural similarity a more distant degree of relationship. On the basis of morphological resemblances we recognize that tigers, leopards, and domestic cats are closely related, that cats, dogs, and horses are much

less closely related, that sweet peas, garden peas, beans, and clovers are close kin and that petunias, pine trees, corn, and sweet potatoes are distant in their biological connections, though they are all seed plants. Close morphological resemblance thus usually indicates close relationship, and close relationship indicates a common ancestor from which the related organisms have arisen. All plants of course are related either closely or distantly to each other; they have diverged from ancestral groups of plants during the geologic eras, in much the same manner as the large branches, then smaller branches and twigs of a tree diverge from a main trunk. The main trunk represents an ancient, ancestral aggregation of plants, from which more recent groups (the branches and twigs) have evolved. The morphological evidences for evolution have been marshalled from a number of sources — from studies of floral morphology, seed structure, wood anatomy, etc. Everywhere the same principles hold — morphological similarity usually (though not always) indicates common ancestry, and common ancestry denotes close relationship.

Developmental Evidence. The series of changes which an individual organism experiences in its development (**ontogeny**) is an important source of evolutionary evidence. Most kinds of plants begin their lives as the products of sexual fusion. A male gamete unites with a female gamete to form a zygote, which marks the beginning of the life of the new individual. As the zygote grows, it follows a series of changes, some of which can be interpreted only as a re-living of ancestral stages through which the particular species has passed in its evolution from an ancestral species (**phylogeny**). This idea is sometimes termed the Biogenetic Hypothesis, and is stated in the familiar form, "Ontogeny recapitulates phylogeny" — that is, the development of an individual follows the course of development of its species. This Biogenetic Hypothesis has been stretched by some biologists unreasonably to explain facts of individual development. Actually an individual organism does not necessarily recapitulate the adult stages of its ancestors, but in many instances merely certain embryonic stages of its forebears. Despite frequent misapplication and exaggeration, the principle of recapitulation is basically sound and has been of great value in the study of evolution of both the individual and of the race. An example of recapitulation in plants is found in the protonema stage in mosses, a phase in the life cycle which apparently indicates the algal ancestry of the mosses. Also, in ferns, the early prothallus is a filamentous structure resembling a filamentous green alga. Another example of recapitu-

lation is found in the living cycads in which the sperms are ciliated, a condition similar to that in ferns and bryophytes in which the sperms swim through the water to the eggs.

Physiological Evidence. Physiological similarities and differences among plants also furnish important information regarding relationships and ancestry. Most fundamental of the physiologic similarities among plants is the ability of green plants to carry on photosynthesis, an attribute which indicates seemingly a common ancestry of all chlorophyllous plants. The presence within certain groups of plants of characteristic chemical substances is another physiologic criterion of close relationship — for example, the aromatic, volatile oils in the plants of the mint family, oils as the characteristic storage foods in the seeds of the lily family, and resinous substances in many members of the pine family. Chemical investigations have shown marked differences among different groups of plants in the presence of certain proteins as characteristic protoplasmic constituents; the closer the relationship among plants, the more nearly alike chemically are their proteins. An entire system of plant classification has actually been proposed upon the basis of the protein characteristics of various plant groups. An interesting illustration of this protein specificity is found in the fact that only certain families of plants have pollen proteins capable of producing hay-fever in man, notably the beech, grass, and composite families.

Evidence from the Study of Inheritance. The study of inheritance in plants has likewise contributed evidence in support of the concept of unceasing change in living organisms. The cross-breeding of plant species frequently results in the production of new types of plants, hybrids which may be propagated indefinitely by vegetative means. Certainly this development of new types of organisms through genetic combinations is a phenomenon involving marked changes, whether or not such changes persist in succeeding generations. In the study of inheritance, biologists have observed the frequent, sudden and unpredictable development of new types of plants from older, parent types; such new types, which are ordinarily relatively permanent and which are passed on in the same form from generation to generation, are termed **mutations** and are considered by some biologists to constitute the principal mechanism of evolution. Mutations have been observed in many groups of plants; numerous mutations have appeared in the evening primroses, the many types of Boston ferns are mutants from ancestral parent ferns, the nectarine is a mutant from a peach, the seedless navel-orange from a seed-producing variety of orange, etc. Various experimental

techniques, for example, the use of X-rays, have made possible the production at will of mutations; among plants, tobacco is especially sensitive to X-ray action and under the influence of this type of radiation has produced numerous mutations.

Evidence from Domestication. In the domestication of plants, man has wrought many changes through hybridization and selection and has also taken advantage of conspicuous mutations in the development of new varieties. Some plants have been so completely altered during the many centuries through which they have been under cultivation that they cannot at present be found in a wild state; that is, they have apparently been changed to such an extent that they no longer show enough similarity to wild plants to be referred to them. In many instances, sufficiently conspicuous similarities or known records of origin exist so that botanists may trace certain domesticated plants to a wild ancestor. For example, the various types of cabbage, kohlrabi, cauliflower, broccoli, and Brussels sprouts may be followed back to a single, ancestral wild-cabbage species, a native plant of Europe. Thus, man through various processes of cultivation and domestication has achieved striking transformations in plants, important evidence of the plasticity of living organisms and their potentiality for change.

Evidence from Geographical Distribution. The study of plant geography has added further evidence in confirmation of the fact of evolution. Many types of plants are widely distributed on the earth's surface, but other species tend to be restricted in their ranges. The fact that different species of plants are frequently found growing under similar climatic conditions in widely separated parts of the world indicates that climatic differences alone cannot explain such distribution. The desert regions of the Southwestern United States and of Western Africa are similar climatically, but the species of plants growing in these regions are very different. Common in the American deserts and lacking in the African are numerous species of cacti, while spurges (*Euphorbia*) abound in the African deserts and are rare in the deserts of the Unites States. Ordinarily, similar species of plants occupy the various areas of a general region. If these areas are separated by barriers, such as high mountains or large bodies of water over which plants cannot pass, the plants in these isolated areas are likely to develop along divergent lines and to become quite distinct. In general, the longer the period of isolation of one region from another, the greater is the degree of difference among the plants of the two regions, as a result of difference in the course of evolution in the separated regions. Some such

explanation as this accounts for the great differences among plants growing under similar conditions but in widely separated and long-isolated parts of the earth. Regions which have been separated from other land areas for a very great period of time usually have floras which are peculiar to them, floras consisting largely of plants found in no other parts of the world. Such regions became isolated very early in the history of life on the earth, and the course of evolution under such prolonged isolation has produced floras different from those of other areas. Examples of long-isolated lands with very characteristic and limited floras are the Hawaiian Islands, the Fiji Islands and other oceanic islands.

Evidence from Intergrading Species. In some genera of plants (e.g., in asters, oaks, roses, willows, and hawthorns), the identification and separation of various species is difficult because of intergrading plants. In these genera most of the individuals of one species may be distinct from most of the individuals of another, related species, but the presence in both of variable plants with more or less transitional or intermediate characters, that is, with characters of both species, renders impossible the erection of a sharp line of demarcation between the two supposed species. If all species were specially created, immutable entities, such intergrading plants could not reasonably be expected to exist. Biologists apply the concept of evolution to these genera which contain intergrading species and regard them as groups in which evolution is actively progressing and in which continuous variation and alteration are occurring. One biologist has somewhat facetiously defined species as "knots on evolutionary threads." This definition means merely that closely related kinds of organisms are not absolutely distinct entities, but that there are tendencies or similarities which extend through many individuals and which are expressed more strikingly in some than in others. Those groups of organisms in which this expression is most pronounced constitute species (knots on the thread). The variable individuals in which the expression is less striking are the intermediate types (the evolutionary threads along which the knots or species are distributed).

6. EVOLUTIONARY TENDENCIES AND DIRECTIONS AMONG PLANTS

Our brief survey of living and extinct representatives of the plant kingdom has indicated clearly that numerous, striking evolutionary changes have occurred in plants during their long residence upon the

earth. The more obvious and more significant of these evolutionary transformations have been discussed in earlier chapters, but are presented again at this point for emphasis and summary, as follows:

1. The transformation of unicellular plants into colonial and multicellular plants, with progressive increase in size and in complexity of structure.

2. The transition from simple, undifferentiated protoplasts to highly specialized protoplasts with nuclei, plastids, and other organized protoplasmic bodies.

3. The origin and evolution of sexual reproduction, possibly from some type of asexual reproduction, as described in the chapter on algae.

4. The evolution of a terrestrial from an aquatic mode of life.

5. The differentiation of vascular, strengthening, storage, and other types of tissues which have made possible successful adaptation to terrestrial conditions.

6. The progressive differentiation of plant organs into distinctly vegetative and distinctly reproductive branches termed cones and flowers.

7. The development of seeds as a result of the retention of gametophytes and the young sporophytes produced from them within sporangial walls.

8. The decrease in size and complexity of the gametophyte generation and the corresponding rise of the sporophyte.

9. The release from dependence upon water for fertilization through the development of pollen tubes in the seed plants.

As stated earlier in this chapter, the most conspicuous tendency in the evolution of plants has been an increase in structural complexity and specialization. This **progressive evolution** has likewise been the principal evolutionary trend in the animal kingdom. Though the course of evolution in both plants and animals has thus been primarily upward, evolutionary changes have not been exclusively progressive, nor have they proceeded at a constant rate. There are many examples among both plants and animals of evolutionary transformations leading toward decreased complexity and simplification from structurally more complex ancestors. Examples of such **retrogressive evolution** are common in the plant kingdom: the probable derivation of higher fungi from algal ancestors as a result of loss of chlorophyll, the development of structurally simplified types of flowers, from more elaborate, more complex flowers (e.g., the evolution of grass flowers from lily-like ancestors), the processes of morphological degeneracy accompanying a
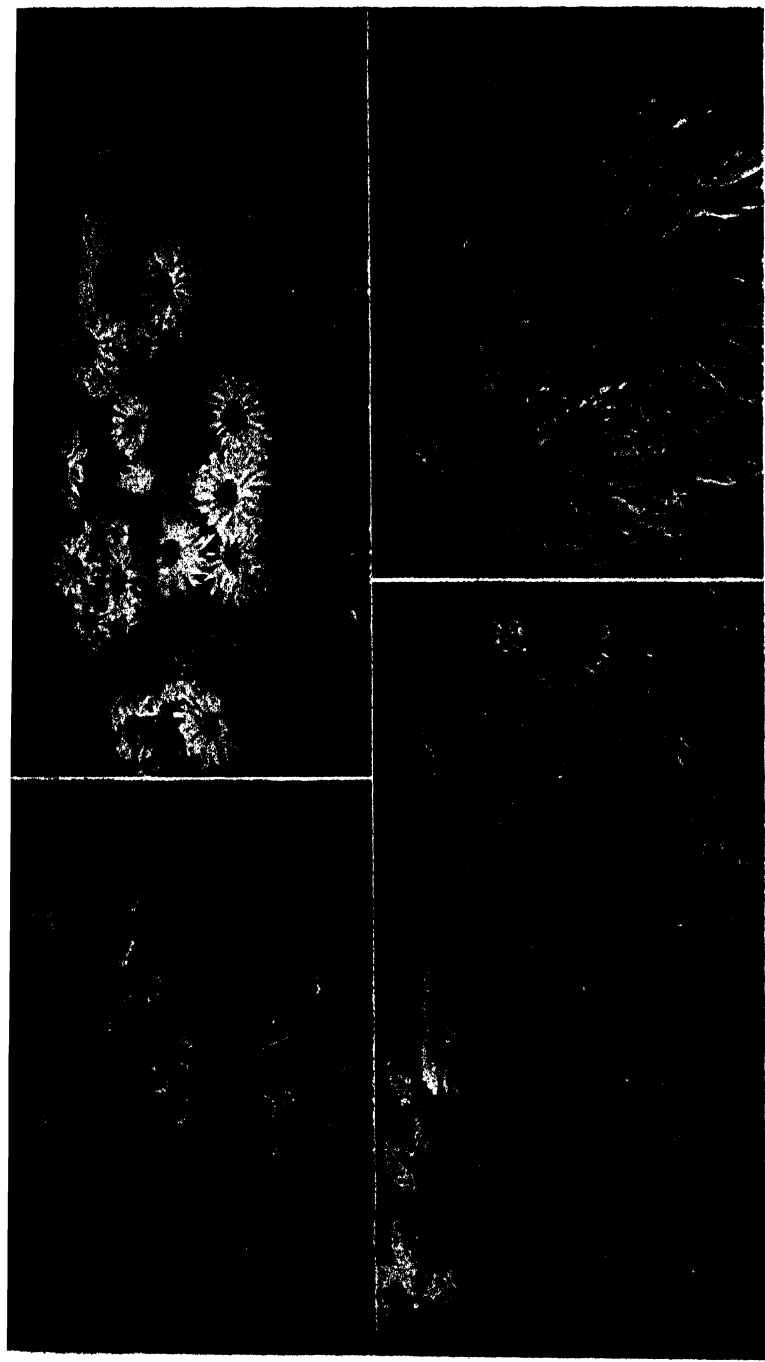
Evolution through domestication. The plant at the upper left is the wild *Chrysanthemum indicum* of China and Japan. The other photographs show cultivated types of chrysanthemums derived from *C. indicum* through hybridization and through selection from endless variations.

transition from an autotrophic to a parasitic mode of life in such flowering plants as mistletoe and dodder are all probably examples of retrogressive evolution in the plant kingdom. Though evolutionary changes of a retrogressive nature have been rather common in certain groups of plants, such changes have been merely sidetracks along the trunk line of progressive evolution and have not appreciably altered the direction of evolutionary advances in the plant kingdom as a whole. In the evolution of different groups of plants, changes frequently occur which follow a common pattern and culminate in similar morphological organization, although the plants which travel such similar paths may be genetically only very distantly related. Such **parallelism** in evolutionary changes is apparent in numerous groups of plants and may occur in both progressive and retrogressive transformations. Among examples of this **parallel evolution** in plants is the retention of gametophytes and the young sporophytes developed therefrom within sporangial walls, a condition found in the seeds of modern seed plants, in club-mosses, in seed-ferns, and various other plants; this evolutionary achievement has thus appeared in different groups in the evolution of the plant kingdom and may be regarded as a type of parallel evolution. Another example of parallel evolution in plants is the morphological reduction which occurs in the transition from an autotrophic to a parasitic or saprophytic mode of life; dodders, beech-drops, mistletoes, and pine-drops are heterotrophic angiosperms which are only distantly related but which have experienced similar modifications in their evolution from autotrophic ancestors — reduction and modification of roots into suckers which penetrate host tissues and rob them of food, reduction of leaves, complete disappearance of or at least marked diminution of chlorophyll, etc. Still another instance of parallel development is the appearance of xylem vessels in the vascular tissues of various rather distantly related groups of plants; vessels are of course common among the angiosperms and have also appeared in a small group of gymnosperms and in some of the pteridophytes.

When parallel evolution proceeds in different plant groups in almost exactly the same manner and under nearly identical conditions, the ultimate products of such evolution may be so similar morphologically as to be distinguished only with great difficulty. This striking condition is sometimes called **convergence,** and the type of parallel evolution which produced it, **convergent evolution.** A conspicuous example of convergent evolution is the development of similar, often nearly identical, xeromorphic characters in very distantly related families of angio-

Fig. 279. Convergent evolution illustrated by

A. *Dyckia altissima* (pineapple family). C. *Haworthia margaritifera* (lily family).
B. *Agave decipiens* (amaryllis family). D. *Aloe humilis* (lily family).
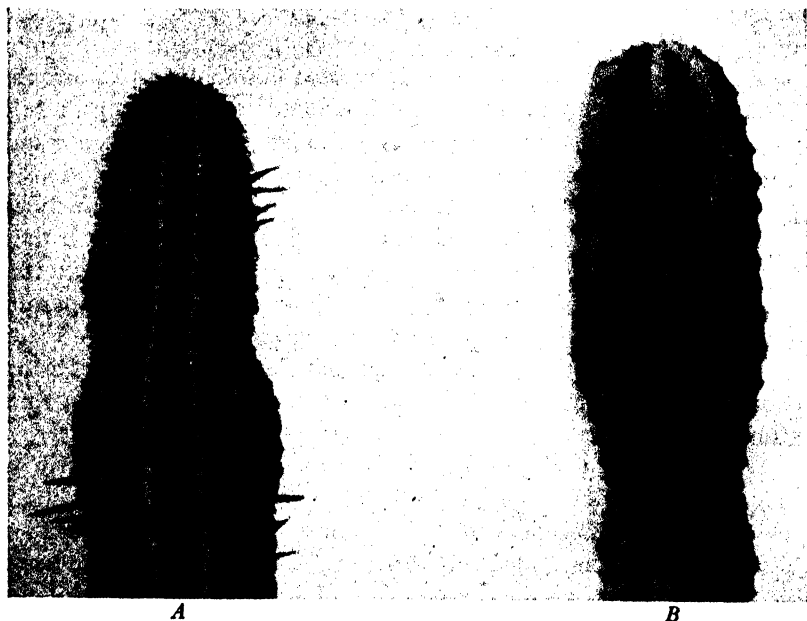
Fig. 280. Convergent evolution illustrated by

A. *Euphorbia cereiformis*, a spurge. B. *Cereus euphorbioides*, a cactus.

sperms (Figure 279). In most species of the cactus family (Figure 280), and in certain desert-inhabiting members of the euphorbia (spurge), lily, milkweed, stone-crop (live-for-ever), and amaryllis families, the formation of heavy layers of cutin, the extensive development of water storage tissues, the reduction of complete disappearance of leaves, and the production of numerous spines or surface hairs are so nearly alike that one is frequently unable to distinguish the members of these several families on the basis of their vegetative morphology. This common pattern of xeromorphism among the members of widely separated families growing in similar or nearly identical environments is one of the most striking examples of convergent evolution in the plant kingdom.

7. THE CAUSES OF EVOLUTION

As indicated earlier in this chapter, biologists agree generally upon the fact of evolution, but differ in their opinions concerning the actual causes of evolutionary changes. These differences of opinion are expressed in numerous theories which have been formulated chiefly within the past century by students of biological evolution.

The Theory of Lamarck. Lamarck, a French biologist, announced in 1801 a theory of evolution which has since become known as The Theory of the Inheritance of Acquired Characters. According to Lamarck, internal forces within living organisms tend to increase the sizes of organisms and their organs; further, each organ or part of an organism is formed at least indirectly, as a result of a need or want, and each organ develops in proportion to the extent to which it is used, continued use gradually strengthening the organ until its fullest development is achieved, lack of use resulting in the diminution of the organ until its complete disappearance. The degree to which an organ is used or not used is determined largely by environmental conditions, the modifications or acquired characters, arising directly as a result of response to external stimuli. The central theme of Lamarck's attempt to explain evolution is the inheritance by offspring of characters which are thus developed in a parent as a result of use or disuse. Lamarck believed that the effects which are produced in organisms as a result of varying environmental conditions are cumulative and that through many generations these cumulative effects result in the production of new species. There is some element of truth in Lamarck's view that the degree of development of certain organs is occasioned in con-

siderable measure by use or disuse (e.g., exercise or lack of exercise), but there is no convincing evidence that developmental changes in-dueed by use or disuse are inherited by offspring. If one tomato plant is grown in a rich soil and another in a poor soil, the former grows more rapidly and produces a greater yield of fruit than the latter; the difference in the growth of the two plants is the direct result of an external factor — namely, the relative degree of soil fertility — but this difference in vigor is not inherited, for seeds from both plants planted in the same kind of soil will grow into plants of essentially the same degree of vigor and metabolic activity. A professional weight-lifter develops unusually large, strong muscles as a result of the practice of his profession, but he does not pass this physical superiority thus acquired on to his offspring.

Many biologists have investigated the possibilities of the direct in-heritance of acquired characters but most of them have found no generally satisfactory evidence in support of Lamarck's theory. En-vironmental factors may modify the body structure of an individual organism, but the bridge between an individual and its offspring is a tiny gamete and unless the environmental factors can modify the hereditary substance carried by the gamete, the acquired characters of the parent are not carried across the gametic bridge to the next generation.

Despite the apparent lack of evidence for the inheritance of acquired characters, some biologists subscribe in part to Lamarck's views; they believe that environmentally induced modifications, if they appear in successive generations as a result of similar environmental conditions operative through long periods of time, may influence the hereditary material of gametes and thus become a part of the heritable characters of a race. If such heritable changes are induced by continued repetition of acquired effects, new kinds of organisms may result and thus the process of evolution may proceed. The many cases of successful adapta-tion in both plants and animals to particular environmental conditions seem to lend weight to this modified Lamarckiañ interpretation of evolutionary causes. It seems difficult to explain, for example, the parallelism in the development of xeromorphic characters in cacti, century plants, stone-crops, and other groups of angiosperms without regard to modifications induced by similar environmental conditions prevailing through long periods of time. Although the hereditary de-terminers of most living organisms are relatively stable, they can be altered under certain conditions. Changes in the genes produced in

some unknown manner are responsible for mutations in nature; and under experimental conditions, for example, by X-ray treatment, genes can be altered. Therefore, it seems not unreasonable to expect that certain environmental factors, less vigorous in their action than X-rays but operative through many years, might effect alterations in the genes of sex-cells and thus lead to the production of heritable changes and concomitantly to new types of organisms.

Thus, Lamarck's theory of evolution insofar as it emphasizes the direct inheritance of acquired characters is generally rejected by modern biologists, although the possibility of the inheritance of environmentally-induced modifications through long periods of time cannot be completely excluded at the present time.

The Theory of Darwin. The theory of organic evolution proposed by Charles Darwin in 1859 and termed the Theory of Natural Selection is so well known that the word Darwinism is frequently (and erroneously) used as a synonym for evolution. As an earlier section of this chapter has indicated, the concept of evolution in human thought may be traced as far back as the philosophers of Ancient Greece and thus is not a theory or idea invented by Darwin. Darwin's name is more intimately connected with the concept of evolution than that of any other man because his researches upon living organisms in relation to evolution have been more extensive and more critically described than those of any other investigator in the history of the evolutionary concept.

Darwin summarizes his own theory succinctly in the following passage from his *Origin of Species:* [The development of species] "has been effected chiefly through the natural selection of numerous, successive, slight, favorable variations, aided in an important manner by the inherited effects of the use and disuse of parts; and in an unimportant manner — that is, in relation to adaptive structures, whether past or present — by the direct action of external conditions and by the variations which seem to us in our ignorance to arise spontaneously."

Thus, Darwin's theory is based upon the following principles:

1. *Overproduction.* Organisms are prodigal in their reproduction and produce far more offspring than can possibly survive. That this principle in Darwin's theory is a fact is recognized by all biologists. A single orchid flower may produce over one million seeds, a single plant of pig-weed (*Amaranthus*) may form 2,000,000 seeds, one mushroom may scatter into the breeze as many as 2,000,000,000 spores. Obviously neither the room nor the food materials necessary for the growth of

these enormous numbers of reproductive structures is available — that is, too many offspring are produced to survive.

2. *Competition.* Because of the limitations of space and of food, all these myriad offspring cannot survive, and they compete with each other for sufficient space in which to grow and for sufficient food materials for their nutrition. Thus, there develops a struggle for existence, not only among organisms of different species, but also among individuals of the same species. Only a small percentage of the offspring is able to win in this struggle and to achieve growth and maturity, the great majority of individuals suffering defeat and death in the combat. This competition acts as a natural check upon the numbers of individuals which attain maturity in different species and results in an equilibrium among the species growing in a particular region, so long as factors tending to disturb this equilibrium do not arise.

3. *Variation.* That individual organisms of the same species are not exactly alike but vary in different degree from other individuals in the species is a long-recognized biological fact. According to Darwin, under a given set of environmental conditions, certain individuals of a species possess variations tending to adjust them very advantageously to these external conditions, whereas other individuals of the same species possess less favorable variations and thus are at a disadvantage in relation to the same set of environmental factors. Those individuals with the more favorable variations, thought Darwin, would be the survivors in the competition for space and nutrients, those with the less fortunate variations would perish. Those individuals with the favorable variations tend to transmit these variations to their offspring; among the offspring, variation again occurs, some individuals surviving, others dying in the struggle for existence; the former then in turn pass on their variations to their offspring, and thus the process continues generation after generation. Darwin considered this "survival of the fittest" as a type of selection, which he termed "natural selection." This process, continuing through many generations, supposedly results in a slow but increasing modification of the species toward characters better suited for survival in the environment. Since only the individuals with favorable variations in the direction of better adaptation to their environment survive and the individuals with the less advantageous variations disappear, in time many new forms of life come into existence, according to the Darwinian theory.

The Darwinian theory of evolution has excited more discussion and disputation than any other evolutionary theory. Many biologists have

supported the theory in its entirety, others have accepted some portions and rejected other parts of it. Certainly Darwin's basic assumptions are true — namely overproduction, competition, variation, the struggle for existence, and the survival of those individuals with the most favorable variations for a particular environment. The most controversial points in Darwin's theory are those of the inheritance of variations and of the degree to which natural selection can lead to significant changes in organisms. It should be emphasized that Darwin himself realized that his theory contained weaknesses and that he believed that natural selection was but *one* factor among several factors operative in evolution.

One objection which has been leveled at Darwin's theory is its failure to account for non-adaptive characters. There is no doubt but that natural selection has accounted for many types of adaptation of organisms to their environments; successful adaptation to an environment implies of course the development and intensification of useful characters for the particular complex of environmental conditions. In addition to such valuable traits, most organisms possess numerous characters which have little or no adaptive significance; in fact, the principal differences which distinguish many species of plants and animals are trifling, non-adaptive characters seemingly of little moment with respect to adjustment or survival. Darwin's theory accounts for the evolution of adaptive characters, but ignores the non-adaptive traits which often constitute the major differences among species.

Another criticism of Darwin's theory may be directed at his failure to distinguish between heritable and non-heritable variations and his assumption that nearly all variations are heritable. Ordinarily, only those variations which are controlled by the chromatin of sex-cells (or in some cases by the cytoplasm of sex-cells) can be transmitted from parent to offspring; many variations are merely direct environmental modifications of somatic or body cells and are not related to hereditary determiners — such variations are not transmitted from generation to generation. Thus, selection based upon somatic or body-cell variations cannot induce changes in the nature of organisms and of course cannot be significant in evolution. Only those variations which are controlled by the hereditary substance, chromatin, of living organisms can be passed on through successive generations.

Another objection to Darwin's Natural Selection Theory involves the phenomenon of over-specialization, as a result of which certain variations have proceeded to so great an extreme that the organisms

in which they occur may actually be impeded or encumbered in the struggle for existence. An example of such extreme specialization is found in *Yucca* flowers, in which the stigma is so peculiarly constructed that only a single kind of insect can effect natural pollination; in the absence of *Yucca* moths, *Yucca* flowers fail to form seeds. Similar conditions obtain in the flowers of *Vanilla* and other genera of orchids. Such structures and behavior have been developed in excess of their greatest usefulness and cannot readily be explained in terms of Darwin's principle of natural selection, according to which successful organisms possess features which provide the most advantageous adaptation to their environments. It is probable that over-specialization has been an important factor in the extinction of many kinds of plants and animals during the course of biological evolution.

One more criticism of Darwin's theory has been made—namely, that it has failed in many instances to distinguish between variations of small magnitude, which do not exceed the limits of normal variability within a species, and variations which are so large as to mark the individuals in which they occur as distinctly new types of organisms. The proponents of this criticism find it difficult to see how appreciable evolutionary changes could be wrought by small, more or less continuous variations, and they emphasize the importance of larger, discontinuous variations in evolutionary processes.

The Mutation Theory. Hugo de Vries, a Dutch botanist, proposed in 1901 a theory to explain the phenomenon of evolution in living organisms. He observed that among plants of species of evening-primrose (*Oenothera lamarckiana*) new types of individuals occasionally developed which were genetically pure — that is, which continued to produce offspring of exactly the same kind through successive generations. Some of these new kinds of evening-primroses were sufficiently distinct from the parent type to be considered new species and have accordingly been named as new species. The sudden, distinct changes which produced these new kinds of plants de Vries called mutations, The ultimate cause of mutations is unknown but obviously it involves changes in the hereditary determiners (genes) of the sex cells of the parent plants. Further, the appearance of mutations is usually sudden and unpredictable. Impressed by the mutants (organisms which arise by mutation) in his evening-primroses, de Vries formulated his Mutation Theory of Evolution, the essential point of which is that new species of organisms are formed by sudden unexplained changes of considerable magnitude (mutations) and that these newly formed

species are distinct from the very instant of their origin. Mutations are sometimes called *discontinuous variations* because they are not connected by series of intermediate forms. In contrast, Darwin's theory emphasized the importance of *continuous variations* which form an unbroken, gradually merging series. De Vries believed that new species arise by mutation and that during the struggle for existence of these newly arisen mutants, natural selection results in the elimination of some and the survival of those better adapted to the environments in which they occur. Thus, de Vries offered what is essentially a modification of Darwin's theory of Natural Selection; he merely altered Darwin's theory on one point, namely, on the nature of variations. Whereas Darwin regarded variations as continuous and intergrading, de Vries considered them discontinuous and distinct. Actually, of course, de Vries' theory merely suggests the importance of mutation as a fundamental process in evolutionary change; it offers no explanation of the ultimate cause of these mutations.

That mutations are to be regarded as outward expressions of alterations in the chromosomal material in nuclei is supported by the discovery of numerous chromosome alterations and aberrations associated with externally visible changes in living organisms. In some plants, the Jimson weed (*Datura*), for example, cell division sometimes fails after the chromosomes have separated in mitosis, as a result of which a cell develops with a chromosome number which is double the normal number. If this happens during reduction division, diploid gametes are formed. If such a gamete fuses with a normal haploid gamete, a **triploid** zygote results; a diploid gamete fusing with another diploid gamete forms a **tetraploid** zygote. If such zygotes develop into mature plants, triploid and tetraploid individuals are the result. Associated with increased numbers of chromosome sets (**polyploidy**) and other chromosomal aberrations are various externally visible or experimentally demonstrable modifications, such as increased size and growth rate of polyploid plants, abnormal flowers, unusually large flowers, varying degrees of sterility, occasionally slower growth, etc. It has recently been discovered that an alkaloid, **colchicine,** applied to plant tissues, is very effective in preventing cell wall formation in cells undergoing mitosis and thus in inducing polyploid conditions. Whether or not polyploidy is an important factor in the development of new species of plants and animals is a matter of dispute at present. In some plants there is evidence that polyploidy may be important in the evolution of new species or varieties; in others, such evidence is lacking. It would

seem on *a priori* grounds that changes in the nature as well as in the number of genes would be a necessary factor in the origin of new species.

Certain objections have been voiced against the Mutation Theory. Chief among these is the fact that mutations, though they arise frequently in certain genera of living organisms, such as *Oenothera* and Boston ferns, are generally rather uncommon and, in certain groups of plants and animals, have never been found. Critics of the Mutation Theory argue that, if mutation were a fundamental cause of species formation, it might be expected to be a much more general phenomenon than it seems to be among living organisms. This objection might be in part refuted by pointing out that the development of new species is also a rather infrequent occurrence and that, although it is infrequent during the span of an investigator's life, it is not an infrequent phenomenon when it is regarded against the background of geological time. That mutation is a mode of species origin in certain groups of organisms is a proven fact, despite the objections which have been offered against de Vries' theory.

8. THE FAMILY TREE OF THE PLANT KINGDOM

As a result of numerous investigations principally of the morphology of fossil and of living plants and of certain other features of living plants, botanists have reached tentative conclusions concerning the probable path of evolution in the plant kingdom. These conclusions are presented in generalized form in Figure 281. This family tree of the plant world should be regarded as an expression of present opinion of most botanists concerning plant evolution, opinions which are based upon the facts of plant relationships as they are now known. Numerous other phylogenetic arrangements have been made in the past and have been altered as new facts about plants have been unearthed; so it is with the present arrangement, which doubtless will in the future undergo changes, as have the earlier representations of plant evolution. Actually, the serious study of plant phylogeny is a relatively young branch of botany and thus many of its tenets are based upon incomplete and scanty data, particularly in the case of those data derived from the study of plant fossils, knowledge of which thus far is exceedingly fragmentary.

The phylogenetic tree indicates the supposed relations and origins
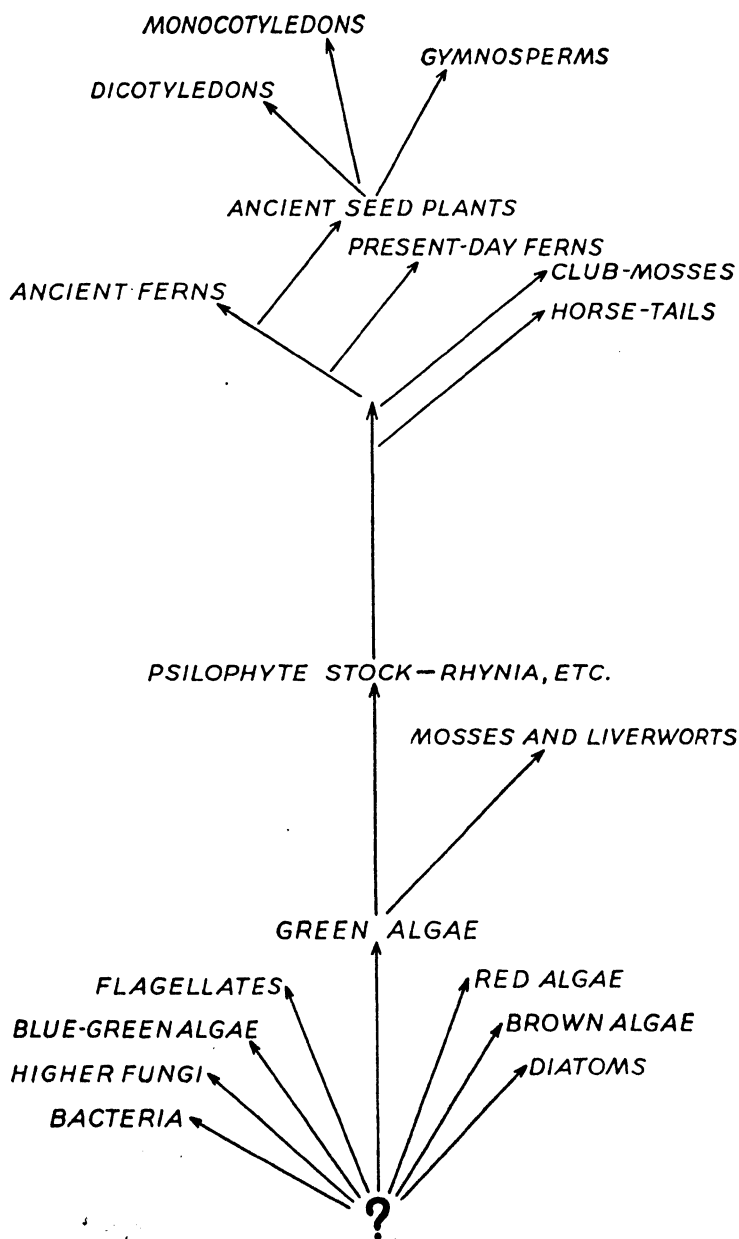
Fig. 281. A simplified phylogenetic tree of the plant kingdom, illustrating the supposed relationships among the major plant groups.

of the major plant groups. Most primitive of all plants are the bacteria, which may have been the first plants to develop on the earth's surface. From the bacteria may have developed the various groups of algae and of higher fungi. The main line of evolution from the thallophytes to higher types of plants is believed to have passed from the flagellates through the green algae to the extinct *Rhynia* (psilophyte) stock. The green algae possibly through some such form as *Coleochaete* are believed to have given rise also to the bryophytes, but at a later time than the period of origin of the psilophytes. The liverworts and mosses are considered by most modern phylogenists to be a terminal evolutionary group — that is, one which has not produced more complex forms of plants; a few botanists still regard the bryophytes as a probable connecting link between algae and pteridophytes, but this opinion does not seem valid in the light of fossil evidence. According to the most modern interpretation of available information, the psilophyte group was probably the first aggregation of true land plants in the earth's history and established morphological tendencies which led, as the diagram shows, to the evolution of the club-mosses, horsetails, ferns, and other types of pteridophytes. From certain types of ancient extinct ferns is supposed to have originated an evolutionary line which culminated in the modern seed plants. It should be emphasized that the gymnosperms and angiosperms are regarded as more or less parallel-groups, that is, groups which have evolved separately from common ancestors along somewhat similar lines. Few botanists at present believe that the modern types of gymnosperms have been the ancestors of the angiosperms, but that these groups have had a common ancestry and certain similar developmental phases. Among the angiosperms, the dicotyledons are believed to have begun their development at a somewhat earlier period than the monocotyledons, which probably evolved from some buttercup-like dicotyledonous ancestors.

Certain generalizations may be derived from a study of the phylogenetic tree. Most striking of these is perhaps the fact that the course of evolution cannot be represented by a straight line along which various groups of plants may be placed but that it is adequately pictured only by a branching system of lines, similar in their positional relationships to the branches of a tree; hence the popular designation of "family tree" for a scheme of phylogenetic picturization. Many of the branches of a family tree represent terminal groups, some of which have become extinct, others of which are living groups that are seemingly static — that is, which have not given rise to other types of plants. The

bryophytes may be considered as examples of the latter kind of terminal group. Another feature of evolution which is clearly illustrated by a phylogenetic tree is the fact that not all of the groups of plants which seem to have appeared in succession along a main evolutionary line have survived to the present time; some of these organisms (e.g., the flagellates) have lived through a large section of geological time, others (e.g., the psilophytes) arose from earlier groups, led to the development of later and more complex types of plants, and then became extinct. Thus, we do not find on the earth living representatives of all the successive members of a continuous evolutionary series; some have survived throughout the period of development of the series, others have lived for a time, carried forward the torch to those newer types of plants better fitted for survival, and have then dropped out of the race.

9. THE PRESENT STATUS OF THE STUDY OF EVOLUTIONARY CAUSES

It is apparent from the above discussion that criticisms may be made of the three most widely known theories of evolution. Each theory is based in part upon recognized biological facts, in part upon assumptions which are not supported in their entirety by observed or experimental evidence. Actually there is no theory at the present time which explains satisfactorily all the phenomena of evolutionary change. A complete explanation of this, one of the most complex processes in living organisms, will be forthcoming only after biologists have uncovered the secrets of simpler phenomena which collectively are involved in the evolutionary process.

Despite their imperfect knowledge of evolutionary causes, biologists have proposed what seem to be rather satisfactory explanations for certain phases of evolutionary change. There is much evidence to indicate that only those changes which influence the hereditary substance of sex cells can actually be transmitted from parent to offspring, although there exists at present no satisfactory explanation of the causes of all such **germinal** variations. Some of these germinal changes (mutations) arise as a result of certain internal forces in living organisms, probably independently of environmental conditions. Mutations frequently develop as a result of alterations in the number of chromosomes or of aberrations in the process of mitosis. Other types of mutations arise apparently as a result of changes in one to several genes and thus

cannot be correlated with visible changes in chromosome behavior. Still other kinds of germinal variations may develop as a result of recombination and segregation of hereditary characters. It is possible that hybridization through long periods of time may account for evolutionary changes, but seemingly mutation is a more potent force in this process.

Many biologists now believe that mutations, of all the variations which occur in living organisms, are most important in the evolution of new types of plants and animals. The process of natural selection operates upon these varying mutations, according to these investigators, eliminating the types of organisms with the variations least suitable to the environment, and fixing the types with the more favorable variations. Thus, there occurs a survival of the fittest mutations, which may be slowly accumulated and transformed into new species in the manner suggested by Darwin. It seems probable, however, that most new species of plants and animals have developed as a result of mutations of sufficient magnitude to distinguish the mutant organisms very clearly from their parents and to mark them as new species.

This modern attempt to explain evolutionary phenomena regards environmental factors as *directive* forces rather than *causative* forces of evolutionary change. The actual changes in organisms are brought about by mutation, and the nature of the environmental conditions under which the organism grows determines which variations will survive, which will perish. Thus, the environment may direct the course of evolutionary transformations, but it is not actually a causative factor in producing variations, which arise as a result of as yet imperfectly understood alterations in the hereditary substance, chromatin, of the sex cells.

There are many additional factors involved in evolutionary phenomena in living organisms. For example, the factor of geographic isolation is important in the development of new types of organisms, for isolation as a result of barriers within the range of a species prevents interbreeding between the individuals in different parts of the general region. Thus, mutations arising in one region may become so isolated or preserved that a new variety or species develops within the isolated area. Darwin and other students of evolution have observed that such isolated areas as oceanic islands and high mountain valleys usually have distinct species of plants and animals peculiar to them and found in no other areas, evidence of the importance of isolation by natural barriers as a factor in species-building. The extent to which the factor

of hybridization has been effective as a cause of evolutionary change is a matter of disagreement among biologists, some of whom believe that cross-breeding between species has produced many of the variations in nature through the introduction of new combinations of characters. Evidence in support of this view is meager, however, so that the possible significance of this process is uncertain.

10. ADAPTATIONS

The term adaptation is frequently employed by biologists in the scientific study of evolution and of the relations of organisms to their environments. It is also popularly used to express a variety of meanings some of which are biologically unsound. In biological usage, an adaptation is a characteristic feature of an organism which adjusts that organism advantageously to the environmental conditions of a given region and makes possible its continued existence under that particular set of conditions. An adaptation may be regarded as the product of a long series of evolutionary changes, resulting from germinal variations and the preservation and isolation of favorable variations as a result of natural selection over a long period of time.

In the study of adaptations, one must avoid the error of attributing foresight and the power of intelligent choice to plants. It is scientifically unsound to say that a plant or a species adapts itself to meet a particular set of environmental factors, for the statement implies the ability of the plant or the species to foresee possible problems arising from a changing environment and to alter its structure or physiological activities accordingly. It is more nearly in accord with our knowledge of the morphology and physiology of plants to say that plants *become* adapted to their environments, not through conscious change, but as a result of the natural selection of germinally induced variations. This viewpoint preserves biological thought from the dangers of a teleological attitude which endows all features of living organisms with the power of purposeful, foresighted activity.

The term adaptation is ordinarily applied to the adjustment between a species and its environment, but in a certain sense the word may be applied to changes wrought in an individual plant by environmental factors. For example, if cabbage plants are grown in a warm greenhouse and are then exposed directly to freezing temperatures for several hours, they are killed. If, however, cabbage plants are grown in a series of gradually decreasing temperatures, remaining at each for

several days, they are able to withstand for several hours temperatures at or even slightly below the freezing point of water. In this case, individual plants have become altered in such a way that they are better adapted (more likely to survive) under a new external condition. This "adaptive" change in the cabbage plants is induced by a changing environment and is not the result of any conscious or directed change on the part of the plants themselves.

▶ Every species of plant actually possesses myriad adaptations, for the very survival of a plant in a particular environment implies an adjustment between the plant and that environment. In many plants adaptive changes have led to rather extreme and conspicuous types of specialization — for example, xeromorphism in cacti and other plants, the structure of the pistil of *Yucca* flowers which can be pollinated only by *Yucca* moths, the pneumatophores of bald cypress trees, the pollinating devices of milkweed, salvia, and orchid flowers, etc.

Adaptations should be regarded as resultants of long series of evolutionary transformations induced as the result of processes of natural selection operating upon germinal variations. Adaptations generally result in more favorable adjustment to a particular environmental complex and as such make possible the survival of species. They should be interpreted as products of natural biological processes, not as the fulfilment of conscious foresight or desire in living organisms.

SUMMARY

1. Fossils are the preserved remains or impressions left in rocks by living organisms. The existence of fossils constitutes one of the chief evidences in support of evolution.

2. The study of fossils shows that different kinds of plants have inhabited the earth in different eras in the earth's history and that the plants of various eras can be related to plants of previous and succeeding eras.

3. It is believed by many biologists that the first living plants on the earth were chemosynthetic bacteria and that subsequent to their development primitive green plants appeared.

4. The earliest plant fossils known are those of certain bacteria and simple algae.

5. The erosion and deposition of sand, clay, and lime and their subsequent hardening into rock led to the formation of sedimentary rocks, usually in the form of horizontal, successively deposited strata, the

more recent ones laid down upon older strata. During these processes, fossils were formed.

6. By studying the rates of erosion, of the deposition of sediments, and other events, geologists have determined the approximate ages of the various rock strata in the earth's crust.

7. The earth's history is divided into five eras: Cenozoic, Mesozoic, Paleozoic, Proterozoic, and Archeozoic. Oldest of these is the Archeozoic, most recent the Cenozoic.

8. No plant fossils have been found in Archeozoic rocks.

9. Doubtful fossils of primitive bacteria and algae have been found in Proterozoic rocks.

10. Numerous fossil algae and some fungi have been found in the rocks of the early portion of the Paleozoic era. Rocks from later strata of the Paleozoic era contain fossils of psilophytes (*Rhynia, Hornea*, etc.), which were probably the first vascular land plants and which may have evolved from algal ancestors, possibly from some green-algal stock.

11. Rocks of the late years of the Paleozoic contain also fossils of plants very similar to our living ferns, horsetails, and club-mosses. Notable among these plants were the "seed ferns," which resembled the ferns in their vegetative structure but which in their reproduction were essentially gymnosperms.

12. The Paleozoic club-mosses, horsetails, ferns, and seed ferns constituted the major portion of the earth's vegetation during the Carboniferous period of the Paleozoic era; their death and partial decay led to the formation of coal.

13. In the closing years of the Paleozoic era, there grew extensive forests of primitive gymnosperms, some of which were the ancestors of our modern living gymnosperms. Also during the latter part of the Paleozoic, many of the ancient pteridophytes became extinct. ·

14. The major evolutionary events of the Paleozoic era were the appearance of land plants and the development of the seed habit.

15. During the early years of the Mesozoic era, there occurred a rapid evolution and diversification of gymnosperms and the disappearance of most of the ancient pteridophytes. The gymnosperms of the Mesozoic era included species very similar to our modern conifers, cycads, and ginkgos. These gymnosperms constituted the major part of the earth's vegetation during most of the Mesozoic era. During the latter part of the Mesozoic era, the first true angiosperms appeared.

16. The Cenozoic era, which includes the present time, may be termed the "age of angiosperms," for these plants have reached their greatest development and have become dominant in the Cenozoic era.

17. The early Cenozoic angiosperms were chiefly woody; herbaceous angiosperms arose later, probably as a result of progressive refrigeration from the earth's poles.

18. Organic evolution includes all the changes which have occurred among living organisms during their history on the earth. Biologists are generally agreed upon the fact of evolution, but disagree upon the causes of evolutionary change.

19. The chief evidences which demonstrate the fact of evolution are:

    a. Evidence from the study of fossils.

    b. Evidence from the study of comparative morphology.

    c. Evidence from the study of comparative development (ongogeny).

    d. Evidence from the study of comparative physiology.

    e. Evidence from the study of inheritance.

    f. Evidence from the study of domestication.

    g. Evidence from the study of geographical distribution.

    h. Evidence from the study of intergrading species.

20. The principal evolutionary changes which have occurred in the plant kingdom are summarized in section 6 of this chapter.

21. Progressive evolution is evolution toward greater structural complexity and specialization. Retrogressive evolution is evolution leading toward decreased complexity and simplification from structurally more complex ancestors. Parallel evolution is evolution which follows a similar sequence of events in distantly related groups of organisms; parallel evolution occurs in both retrogressive and progressive changes. Convergent evolution is a term applied to an extreme type of parallel evolution which results in the development in different groups of organisms of individuals which are morphologically almost indistinguishable.

22. The following are the most prominent of the theories which have attempted to explain the facts of evolution:

    a. The Theory of Lamarck is based upon the belief that evolution results from the inheritance by offspring of characters which are developed in their parents as a result of use or disuse, use of an organ tending to accelerate its development, disuse tending to cause it to decrease or to disappear.

    b. The Theory of Darwin is based upon the facts of overproduction, of limited food, of competition, of variation, and of the elimination of organisms with unfavorable variations in the struggle for existence. According to Darwin, organisms with favorable variations pass these variations on to their offspring. This process, continuing through many generations, supposedly results in the modification of species. Darwin's theory is sometimes called the Theory of Natural Selection.

c. The Mutation Theory of de Vries holds that evolution occurs as a result of the appearance of sudden, distinct changes, called mutations. These develop as a result of changes in the genes, or hereditary determiners in living organisms. Mutations are heritable, and if they are of sufficient magnitude, they result in the formation of new species.

23. A proposed phylogenetic tree of the plant kingdom is presented in this chapter.

24. A modern theory of evolution, supported by many biologists, holds that the changes which arise in living organisms are principally mutations and that natural selection operates among these mutations, eliminating those organisms with unfavorable mutations and allowing a survival of organisms with favorable mutations. Such an explanation includes features of both de Vries' and Darwin's theories.

25. Adaptations may be regarded as adjustments of living organisms to their environments and as products of long series of evolutionary change, resulting probably from mutations and the preservation and isolation of favorable variations as a result of natural selection.

The Distribution of Plants in Space: the Relation of Plants to Their Environments

1. THE STUDY OF ECOLOGY

As DESCRIBED in the chapter on growth and responses, plants are dynamic, living organisms which possess the fundamental protoplasmic property of irritability and which are thus sensitive to the continually shifting factors surrounding them. These external conditions of environments cause varied types of responses in plants; they influence the rate of growth of certain plant tissues and organs, they initiate internal changes which result in movements of leaves, stems, roots, and other parts of plants, and they directly affect the rates at which various physiological activities proceed. A living organism is after all an infinitely complex mechanism, the efficient functioning of which is dependent in large degree upon the nature and quantity of energy available for its operation, upon processes of repair and replacement of worn-out parts, and upon other intricate external and internal relationships. The myriad environmental factors to which plants are sensitive influence not only the rates of growth and spatial adjustments of individual plants and their parts, but they also influence the distribution upon the earth of the masses of individuals which constitute a species. Every species of plant *seems* to be fitted to a particular set of environment circumstances, within the limits of which it is able to grow and reproduce its own kind. Many species of plants are exceedingly plastic and thrive even under wide ranges of environmental conditions; tolerance of many types of environments is an unfortunate characteristic of many cosmopolitan species of obnoxious weeds, plants which appear in places where they are not wanted and which grow and reproduce in many climates and in many types of soils. Other species are less flexible and can prosper only within

narrow limits of environmental variations; many ferns, for example, azaleas, rhododendrons, California redwood trees and numerous other kinds of plants are adjusted to narrow ranges of variations in light intensity, soil acidity, atmospheric humidity, and other external factors, and are unable to survive if changes in these factors exceed the limits of the range to which these plants are adapted.

The study of the environmental relations of plants is termed **ecology.** This branch of plant science seeks to determine the effects of environmental factors upon the growth, distribution, migration, fecundity, and other aspects of the relationships of plants to these factors and to each other. Ecology aims also, through applications of its body of knowledge concerning the effects of environmental conditions upon plants, to give aid to the science of conservation of natural resources and thus contributes to such phases of conservation as the control of soil erosion, reforestation, restoration of wild animal life, the restoration of grassland vegetation, flood control, etc., all of which are fundamentally ecological problems.

The science of ecology is one of the most expansive and intricate fields of biology; it involves the consideration of exceedingly complex factors and relationships and its searching and discriminating study requires extensive field experience and a formidable background in taxonomy, plant physiology, chemistry, physics, geography, geology, mathematics (with particular emphasis upon statistical procedures), meteorology, and soil science. For these reasons it is obvious that a treatment of ecology in an elementary course in botany must be generalized and inevitably superficial.

2. THE FACTORS WHICH INFLUENCE PLANT DISTRIBUTION

One of the most striking features of plant life is the fact that different kinds of plants grow in different places under different types of environmental conditions. Black willows, for example, grow principally along the banks of streams and the margins of lakes; cattails thrive only in swamps or in the marshy borders of lakes or in moist ditches; sunflowers are characteristic plants of open, sunshiny, moderately dry regions, and cacti are typically inhabitants of arid and semi-arid areas. As indicated in the preceding section of this chapter, every kind of living organism represents an intricate adjustment between its structure

and physiological activities, and its environment. This adjustment which renders each kind of organism especially fitted to a particular range of environmental factors is usually termed **adaptation** and may be considered in part an expression of the evolutionary experiences of the species.

The factors which have been, or are, important in determining the distribution of different kinds of plants may be classified into two major groups:

I. **Contemporary factors** — that is, factors which at the present time are affecting the growth, reactions, and distribution of living plants. These factors may be separated into three groups:

    a. **Climatic factors** — those which act upon plants through the atmosphere: light, precipitation, and temperature.

    b. **Edaphic factors** — those which act upon plants through soils: the physical properties of soils, drainage, water-holding power of soils, the chemical nature of soils, etc.

    c. **Biotic factors** — those which involve relations with other kinds of plants and with animals.

II. **Factors of the past.** As described in the chapter on evolution, the distribution of plants on the earth is in part a result of major geological transformations in the earth's history. The fact that long-isolated islands, such as those of Hawaii, have floras which are very different from floras in other parts of the world; the great similarities between the plants of the more southerly islands of the West Indies and those of the north coast of South America; the occurrence in the climatically similar desert regions of the Southwestern United States and of South Africa of entirely different species of plants; and the fact that certain species of plants which grow in the high Alps of Europe also grow in the far north of Norway and Sweden but not in the intervening areas are a few examples of features of plant distribution which can be explained only upon the basis of geological phenomena of past geological ages. Among the important geological events · which have markedly influenced the distribution of plants were the upthrust of high mountain ranges, the emergence and subsidence of land masses beneath the surfaces of seas, and the advance and retreat of glaciers. These geological phenomena have resulted in the formation of barriers and highways which have restricted or facilitated the dispersal of various species of plants, and they have frequently brought about changes which have resulted in the complete extinction of many species in certain regions. In the study of distribution of plants, particularly

over rather large areas, a knowledge of the geological history of the areas under consideration is prerequisite to an adequate interpretation of the observed facts of distribution.

In this discussion of factors influencing plant distribution, emphasis will be placed upon the contemporary ecological factors.

3. CLIMATIC FACTORS

The climatic factors which are most influential in affecting the distribution of plants are temperature and moisture. It is well known that different kinds of plants grow best and survive within different ranges of temperature. Thus, many temperate zone trees and shrubs are commonly able to endure high summer and low winter temperatures, while woody plants from the tropics are killed quickly when the temperatures to which they are exposed are in the vicinity of the freezing point of water. In most plants, the minimum and maximum temperatures through which active physiological processes continue are in the vicinity of 34° F. to 110° F. respectively. When temperatures fall below or rise above these limits, ordinarily physiological derangements occur which result in injury or death. Temperature variations influence the ratio of all physiological processes and may even affect them qualitatively. The production of flowers and the formation of seeds in many species of plants are likewise directly influenced by temperature conditions of the environment. Thus, temperature may be a factor in determining survival or extinction of plants within a given area, in part through direct effects upon vegetative processes, in part through its influence upon reproductive activities. For example, in Illinois, mistletoe, which is very sensitive to low temperatures, grows only in the extreme southern part of the state. Following unusually mild winters, mistletoe plants extend their ranges as much as eighty miles farther north. Severe winters kill the plants, which have begun to grow in more northerly districts after mild winters, and thus fix the northern limit of the mistletoe at the extreme southern end of the state. Temperature variations are among the most important of all ecological factors and determine in large part the distribution of plants over large regions of the earth. Thus we find the most lush and most varied vegetation in warm equatorial regions, with gradual reduction in the luxuriance and variety of plant life toward the poles. Within smaller, more restricted areas, temperature variations are ordinarily rather slight and thus are not so important ecologically as are other environmental factors.

That plants require large quantities of water in their growth and development and that the distribution of plants is in large degree related to available moisture are patent. Plants vary greatly in their water requirements, some species thriving in regions with an annual rainfall of less than 4 inches, others growing only when they are submerged in water. The moisture which plants absorb from soils comes ultimately from rain or snow, or in some regions, from both. Both the total annual amount of precipitation in a given region and the distribution of this precipitation through the year are important in influencing the distribution of plants. For example, in those regions of the tropics in which the rainfall is heavy and rather equally distributed throughout the year, the vegetation is usually evergreen and consists of plants which are rather uniformly physiologically active throughout the year. In those areas of the tropics, in which an equally heavy annual rainfall is unevenly distributed between a marked wet and a pronounced dry season, the species of plants are usually deciduous — that is, they lose their leaves during the dry season, through which they are in a relatively dormant condition, and develop leaves and become physiologically very active during the wet season. As indicated in the chapter on soils and roots, only a portion of the water which reaches soils is available to plants. The nature of the soil, its water-holding power, its drainage, slope, percentage of colloidal material, and numerous other factors are intimately involved in determining the degree to which precipitated moisture may actually be held in the soil spaces and used by plants. A sandy or gravelly soil from which water drains away rapidly and which is thus unable to retain water is a dry soil, regardless of the amount of rainfall which may reach it, while a rich loamy soil with smaller particles, a rather high content of water-holding colloidal materials, and slow drainage may provide a moist substratum for plant growth even in regions with moderate amounts of precipitation.

Light influences the growth and distribution of plants through its effects upon transpiration, photosynthesis, enzyme action, the production of flowers, soil temperatures, rate of water absorption, and upon numerous other processes. Light is ordinarily less important than temperature and moisture in influencing the distribution of plants over wide regions, but within limited areas, as for example, on a hillside, a forest floor, or in a deep ravine, it is an exceedingly important factor. Just as they are variously adjusted to differences in temperature and moisture, different species of plants are likewise adapted to different ranges of light intensity and duration. Many plants thrive only in diffuse

light which has only 15 to 25 percent the intensity of full sunlight in that region; among such **photophobic** plants are many species of ferns, mosses, and liverworts, and many late spring- and summer-blooming woodland wildflowers, such as lady-slipper orchids, wood-sorrel, hydrophyllums, figworts, and geraniums. Numerous **photophilic** species grow best and produce abundant seed only when they grow in exposed situations in bright sunlight; prominent among such species are numerous grasses, such as buffalo grass, big bluestem, and Indian grass, many composites, such as sunflowers, rosin weeds, cone-flowers, and partheniums, and many members of the milkweed, spurge, and legume families.

The different reactions of various species of plants to differences of light intensity are important factors in determining the kinds of plants which become dominant within a limited area and in influencing certain cultivation practices. For example, in the Pacific Northwest, Douglas fir and Western hemlock trees grow in the same extensive forest areas. The hemlocks are shade-tolerant trees which grow well in reduced light, whereas the Douglas firs thrive only under higher light intensities. Therefore, when a forested area is lumbered, nearly all the trees, large and small, are cut away, for to leave the smaller trees growing in large numbers would shade the forest floor to such an extent that the hemlocks would thrive and the Douglas firs would be unable to grow. This result is undesirable, for hemlocks are much less valuable commercially than Douglas firs. Therefore, in order to ensure a continuous production of Douglas fir trees in a given area, lumbermen cut out most of the smaller trees, as well as the larger, commercially valuable ones, so that the forest floor and the Douglas fir seedlings growing on it, may be brightly illuminated by the direct rays of the sun. Similarly, the original forests of Denmark were composed largely of oaks, with smaller numbers of beeches, which are shade-tolerant and able to grow successfully in dense forest shade. When the larger oaks were cut out, many of the beeches were allowed to remain, with the result that the oaks have almost completely disappeared, for oaks are able to thrive only under rather bright illumination. The canopy of beeches prevented the oak seedlings on the forest floor from obtaining sufficiently bright light; the oaks have thus been replaced almost entirely by beeches.

Light exerts an important effect upon plant distribution through its influence upon reproduction in flowering plants. Plants of the high north and south latitudes (e.g., Canada, Alaska, northern Russia, Argentina, etc.) are principally long-day plants which flower only

during the very long days of the summers of those regions. Plants of lower latitudes — for example, of equatorial and near-equatorial regions, are principally short-day plants which blossom at various times of the year; in these seasons the days vary but little in length from season to season. Short-day annuals are ordinarily unable to flower and reproduce when they are grown in high latitudes, and, in like fashion, long-day plants of high latitudes usually do not flower when they grow under the short-day conditions of lower latitude. Thus, light duration influences the production of seeds in many plants and accordingly exerts striking distributional effects.

Another atmospheric factor of some degree of importance in influencing the distribution of plants is wind. At high mountain elevations and similar exposed positions, strong winds may exert marked mechanical effects upon plants, bending and twisting them grotesquely. High wind velocity, coupled with low winter temperatures and consequent difficulty of water absorption, is the principal factor which sets the upper limit (timber line) at which trees are able to grow, and is thus an important ecological factor. The major physiological effect of wind upon plants is to increase their rates of transpiration. Plants are able to grow successfully only so long as they can balance their water income with water outgo. If transpiration exceeds absorption for a prolonged period, wilting and death are inevitable. Plants vary greatly in the degree to which they can maintain this balance; those species which are most sensitive to the drying effects of winds and which are unable to increase their rate of water absorption are less likely to survive than species which are less susceptible to wind action and which are able to absorb water more effectively from the soil. Winds may also influence the distribution of plants through their effects upon the soil or sand in which plants are growing. High winds cause shifting of light soils and sands and thus prevent many kinds of plants from becoming established in such substrata. Ordinarily only perennials with deep, much-branched roots and with well-developed underground rhizomes or stolons grow successfully upon sand dunes and other types of shifting soils.

4. EDAPHIC FACTORS

Edaphic factors are those which act upon plants through the soil. These have been discussed in part in the preceding section of this chapter and in the chapter on roots and soils and at this point will be
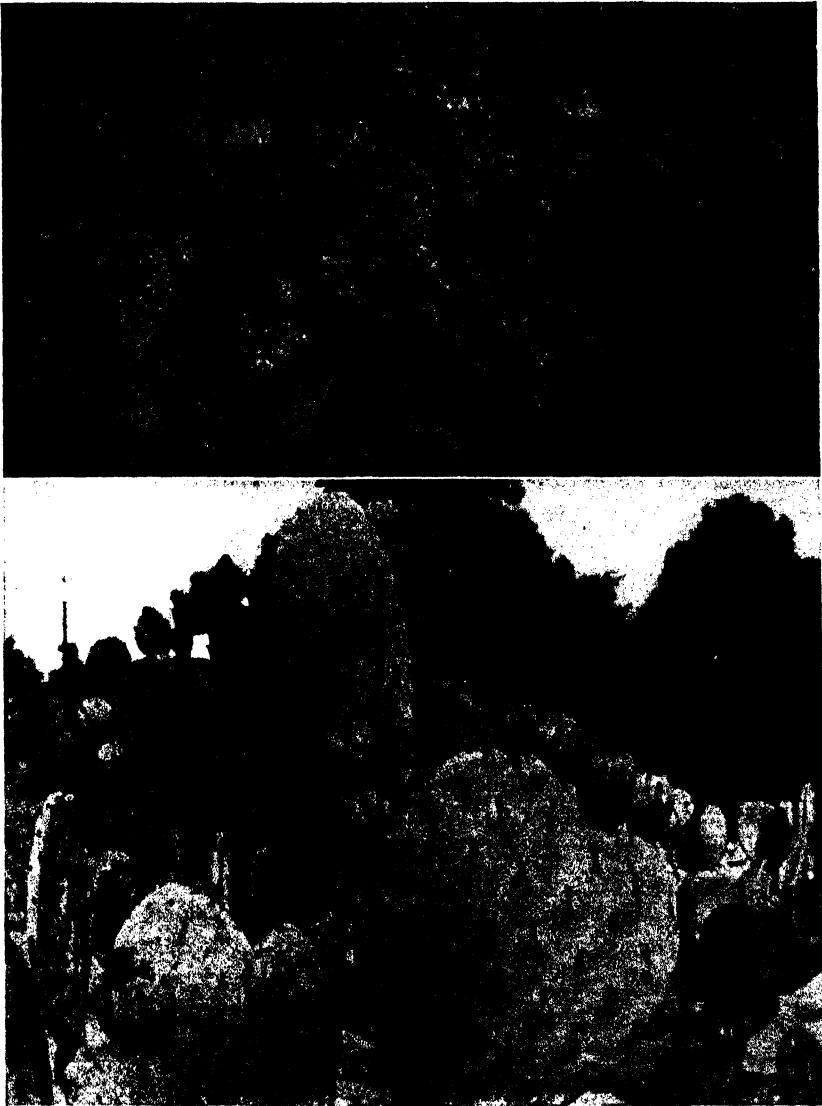
Fig. 282. Cactus plants are true xerophytes

A. *Opuntia* in flower. (Photo by C. J. Alexopoulos)
B. *Opuntia Dilleni* stems, with fruits.

Fig. 283. Cattail (*Typha*), a common hydrophyte.

but briefly summarized. Important among the edaphic factors is the amount of available water in the soil; the availability of moisture is influenced by many conditions, the principal ones of which are the distance of the standing water (water table) below the surface of the soil, the rate at which water percolates downward through the soil, the sizes of soil particles, the amount of colloidally dispersed substances in the soil, the slope of the soil surface, the amount of annual precipitation, and the distribution of precipitation through the year. The relationships between plant growth and the available-water content of soils are so striking that plants may be grouped into four categories, already described (on the basis of these relationships), namely, **xerophytes** (Figure 282), which live under conditions of scanty available soil moisture (examples: cacti, Russian thistle, Yuccas, sagebrush); **hydrophytes** (Figures 283, 284), which live in water or very wet soils (examples: cattails, water-lilies, *Elodea*, pond-weeds); **mesophytes** (Figure 285), which grow in soils with moderate supplies of available moisture; and **halophytes,** which grow in soils which may contain abundant water but which have such a high concentration of salts in the soil solution that plants are able to absorb water only with difficulty (examples: saltbush, greasewood).

Another edaphic factor which influences the growth and distribution of plants is the reaction of the soil — that is, its degree of acidity or alkalinity. Certain species (for example, many ferns, beech trees, saltbush) grow only in soils which are slightly or very alkaline, others (sour dock, heathers, rhododendrons) thrive only in soils of acid reaction. Most species of plants are rather tolerant and are able to grow over a wide range of soil reactions.

The nature of the soil solutes is also important from the nutritional
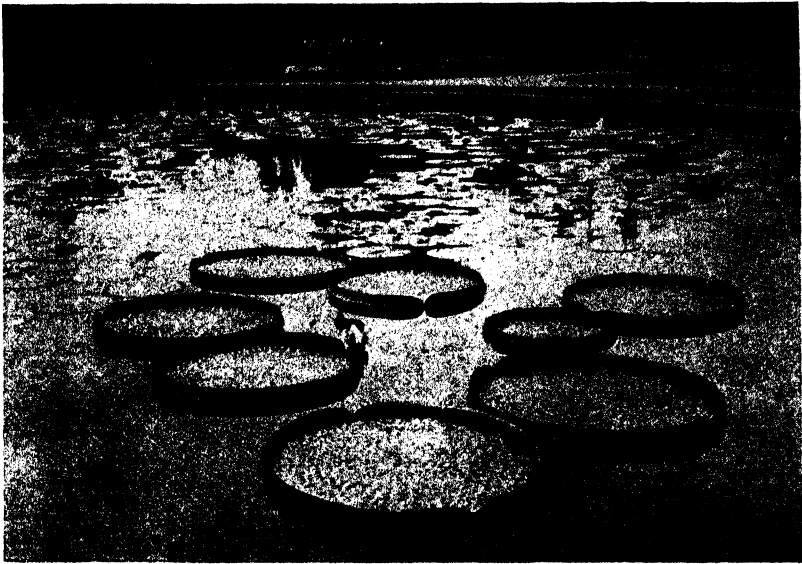
Fig. 284. Water-lilies (*Victoria* and *Nymphaea*), true hydrophytes.

standpoint. Only when all of the essential chemical ions are present can green plants grow in normal fashion. Although all species of green plants apparently require the same ions for their normal development, different species require them in varying quantities, as a result of which certain soils commonly support the growth of some species of plants better than they do others.

Soil temperatures constitute another soil factor of importance in the ecological relationships of plants, particularly when temperatures are low, for low temperatures reduce the rate of absorption of water and solutes by roots and thus may bring about serious physiological derangements within plants. One of the reasons why many kinds of evergreen trees cannot be successfully grown in those parts of the middle latitudes with only moderately cold winters is the fact that air temperatures on winter days are frequently high enough to promote rather rapid transpiration, while soil temperatures are sufficiently low to retard water absorption. In such circumstances, evergreen trees frequently grow very slowly or die as a result of an excess of water outgo over water income. Soil temperatures are affected by air temperatures, the intensity of sunlight, the angle at which sunlight strikes the soil, the daily duration of sunlight, the amount of moisture in the soil, etc.

Fig. 285. Mesophytes in a northern coniferous forest. Ontario.

The air content of soils is an edaphic factor of great importance, particularly with reference to root growth and seed germination. Actively growing roots require oxygen in considerable quantities for their respiration and usually become stunted or otherwise abnormal when the oxygen content of the soil is reduced. The roots of most meso-phytes and xerophytes are especially sensitive to oxygen deficiencies in soils, whereas the roots of most species of hydrophytes are able to grow in apparently normal fashion even when the oxygen supply of the sub-stratum is very low. The oxygen content of soils is also an important factor in seed germination, for germinating seeds respire rapidly and ordinarily require large amounts of oxygen. Again, hydrophytes are somewhat an exception to this generalization, for many of them (e.g., water-lilies, cattails) have seeds which are able to germinate in very low oxygen concentrations which would inhibit the sprouting of seeds of most other species of plants.

5. BIOTIC FACTORS

The growth and development of every kind of living organism is influenced by the activities of other living organisms as well as by

climatic and edaphic factors. These biotic relationships are the most complex to be found in the myriad ecological phenomena of living organisms. Not only do various species of plants affect the development of other species, but there are also intimate interrelations between plants and animals. Thus, any ecological investigation which concentrates upon plants and neglects the relations of those plants with animals can present what is at best an incomplete analysis. Similarly, an animal ecologist who fails to consider plants in his studies of animal behavior can see only a limited portion of nature's canvas.

The biotic factors of ecology are so intricate and so numerous that only the more striking examples of them can be considered in an elementary textbook. One of the most common biotic relationships among living organisms is that found in **competition.** Individual plants of the same species and plants of different species compete with each other for water, for mineral nutrients, for space, and for light. The plants in a forest compete for light, and the plants which grow more slowly are shaded by more rapidly-growing individuals and often die as a result of their inability to obtain sufficient light. As a result of competition for moisture in the soil, those plants which absorb water most rapidly usually survive, whereas those which take up moisture more slowly are likely to succumb in the competition. One of the reasons why weeds are undesirable is the fact that many of them absorb large quantities of water and thus rob the soil of moisture which might be absorbed and used by the cultivated plants with which the weeds compete. Morphological features, such as depth of root systems, numbers of root branches, and development of water storage tissues, and physiological characteristics, such as rate of transpiration, rate of water absorption, rate of shoot growth, and photosynthetic efficiency are factors which determine what species of plants will survive under a given set of environmental conditions and what species will lose out in the competition.

Parasitism is a biotic relationship which influences strikingly the development and distribution of plants. Serious infections by virulent fungous parasites interfere seriously with photosynthetic activity and thus indirectly reduce the numbers and quality of seeds produced, a result which in turn retards the efficiency with which the infected plants propagate themselves. Especially serious parasites, such as the chestnut blight fungus and the Dutch elm disease fungus, have changed the ecological picture in various regions of the world by destroying completely all of their host plants within limited areas. The numerous and

varied relationships between parasites and their hosts constitute large and important fields of both plant pathology and ecology.

Akin to parasitic relationships are symbiotic relationships. The term symbiosis merely means "living together" and in this sense may be applied to all living organisms, for all plants and animals live together in some degree. "Symbiosis" is commonly used in a more restricted sense, however, to refer to an intimate biotic association in which the organisms which live together occur in this relationship more commonly than they live apart and in which the relationship is often mutually beneficial. Lichens, described in the chapter on fungi, are regarded as symbiotic associations of algae and fungi, and the nitrogen-fixing bacteria which inhabit the nodules of leguminous roots live apparently in a symbiotic relationship of mutual benefit with their hosts.

Animals constitute an important biotic factor which influences the growth and distribution of plants, for all animals are dependent directly or indirectly upon plants for food. Overgrazing of grasslands and forests by cattle, deer, bison, and other animals produces marked vegetational changes. When leaves are continually cropped, the food-making machinery of plants is destroyed and plants starve and die. Further, the mechanical effects of sharp, pounding hoofs dig up sod and destroy the vegetation. When valuable forage plants are thus destroyed, other, less desirable kinds of plants, such as wild mustard, tar-weeds, Russian thistle, and species of true thistles, commonly replace them. These weeds are of little value as forage plants for animals, they do not hold the soil effectively, they are frequently poisonous or otherwise injurious to domesticated animals, and once they become established they offer serious competition to more valuable types of plants and either crowd them out completely or prevent their return. An interesting example of the complex interrelationships of plants and animals may be found in the overgrazing of considerable areas by deer in the Grand Canyon National Park. With the opening of the park to tourists, the park rangers had killed many of the mountain lions which formerly were in the area and which preyed upon deer. The destruction of the lions has removed a natural check upon the deer population, which has increased enormously and has therefore taxed the natural feeding resources of the park to their limit. Animals are also important biotically as carriers of many kinds of seeds, as has been pointed out in the discussion of seed dispersal in an earlier chapter. Birds eat many types of seeds, some of which pass through their digestive tracts and are distributed in their feces. Animals with furry coats frequently carry the

spiny or barbed seeds and fruits of cockle-bur, tick-trefoil, beggar-ticks, and many other kinds of plants for great distances and thus unwittingly (sometimes probably wittingly if they brush against seeds with very large and sharp spines!) distribute plants over considerable areas.

The presence or absence of suitable flower-pollinating insects is an important biotic factor influencing the distribution of plants, for most species of angiosperms are insect-pollinated and are therefore dependent upon pollinating insects for their production of seeds. Fluctuations of insect populations thus markedly affect the seed crop of many species of plants and thus influence the degree to which plants may propagate themselves.

Man is one of the most effective biotic agencies related to the dispersal and distribution of plants. In his migrations and commerce he has made cosmopolites of plants which were formerly very provincial and limited in their distribution. Students should refer to the table at the end of Chapter XVII for a list of plants formerly of limited range but nearly worldwide in their distribution as a result of man's transporting them knowingly or unwittingly to new parts of the world.

Among the most intricate biotic relationships of plants are those between bacteria and higher plants. Green plants are the synthetic organisms of the world; they alone (except for a few species of chemosynthetic bacteria) are able to fashion carbohydrates, fats, proteins, and numerous other complex organic substances from carbon dioxide, water, and inorganic mineral substances of the soil. The saprophytic bacteria may be regarded as organisms which reverse the synthetic activities of green plants, for they attack the complex substances which constitute the bodies of plants and animals and their wastes, and break them down in processes of decay, which ultimately restore the simple substances, used by green plants in their synthetic activities, to the air and the soil. There are many types of saprophytic bacteria (together with a number of saprophytic higher fungi) which carry on these processes of decomposition, the end products of which are principally water, carbon dioxide, ammonia, hydrogen, nitrogen, methane, and hydrogen sulfide. The water and carbon dioxide are used by green plants in photosynthesis, hydrogen, methane, and hydrogen sulfide are oxidized by chemosynthetic bacteria, which derive their energy for food syntheses from such oxidation. The free nitrogen is fixed by the activities of free-living and symbiotic nitrogen-fixing bacteria, and the ammonia is converted by various groups of bacteria through a series of compounds to nitrates, which are the nitrogen compounds most

Fig. 286. The carbon-nitrogen cycle.

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Fig. 287. *Tillandsia* (Spanish moss), an epiphyte growing on the branches of trees. *Tillandsia* is a member of the pineapple family.

readily absorbed and used by green plants. These complex transformations are pictured in Figure 286, which represents the nitrogen-carbon cycle in nature.

Another interesting biotic relationship is seen in the growth of **epiphytes** (Figure 287) upon other plants. Epiphytes are the hitch-hikers of the plant world; they grow upon the limbs of trees and other plants, upon telephone poles, wires, roofs of buildings, etc., particularly in warm, humid regions. Most epiphytes are autotrophic plants, that is, they are able to manufacture their own food and do not rob the plants upon which they grow of food. They obtain carbon dioxide and a certain amount of moisture from humid air; and their roots absorb water and minerals from the wind-borne debris which collects about them and in the crevices of the bark over which they grow. Many species of orchids, mosses, ferns, lichens, and members of the pineapple family are epiphytes. Though most epiphytes do not take food from the bodies of the plants upon which they grow, they may constitute a source of injury. for they shade the leaves of their supporting plants

and frequently because of their weight cause limbs of the supporting plants to break and fall.

6. PLANT ASSOCIATIONS AND THEIR BEHAVIOR

A group of plants which live together under the same complex environmental conditions is called a **plant association** or **community.** Ordinarily, many species are present in an association, but usually most of the individual plants present belong to a few dominant species, the names of which are used to characterize the whole community. Thus, we speak of a water-lily community, a spruce-balsam forest, an oak-hickory community, or a beech-maple-hemlock community. The species of plants which are commonly present together in a community are associated because the particular set of environmental conditions in which they grow are more favorable for their development than they are for other species of plants. In many instances, however, any one of a number of communities composed of different groups of species might be able to grow under a particular set of environmental circumstances; in such cases, priority of colonization is an important factor in determining which community prevails. As environmental conditions change, various members of a community, unable to thrive under the new conditions, disappear and may be replaced by other species better adapted to life in the changed environment.

A community is not a static group of organisms, but continually undergoes alterations as environmental factors change. A community is like an individual plant or animal in that it has a beginning, grows, invades other communities, competes with them and may then retreat and die. During its development, it may experience seasonal rhythms, annual cycles, and regular fluctuations over longer periods of time. Not only is a community influenced and controlled by the environment in which it develops, but it may in turn affect the environment; for example, a community may alter wind velocity, atmospheric conditions, and light factors in its immediate environment, and also may bring about modifications in the physical and chemical properties of the soil in which it grows, for root growth loosens soils, carbon dioxide excreted by roots aids in the decomposition of rock particles, and the death and decomposition of leaves and other plant parts adds various substances to the soil.

One of the striking dynamic aspects of the development of a com-

munity is its tendency to spread and to invade other communities. A particular community is limited in large degree by the conditions of its environment. If the seeds of the plants of a community are carried to other areas the environmental conditions of which are much like those of the community from which the seeds came, an extension of the parent community may take place. The species of the parent community may be said to have invaded a new area. During the course of such invasion, the invading species must compete for water, minerals, light, and space with other plants already present in the invaded area. If the conditions of the environment favor the invading species, then those species may become dominant in the extended community and the original inhabitants of the invaded region are dominated by the invaders, often to the point of extinction in that particular region. Many species of weeds, tolerant of wide variations in environmental conditions, have been successful invaders of new areas, as a result of the natural dispersal of their seeds or their being transported accidentally by man to new regions. The existence of similar environmental conditions in different places does not guarantee the presence of the same kind of community in these regions, for there are natural barriers, such as high mountain ranges, oceans, glaciers, and deserts, which prevent communities from invading other areas.

A plant community or association is not a permanent feature of a particular environment. Changing environmental conditions, some of which are brought about by the community itself, result in continuous changes in the nature of the vegetation occupying a region. During a period of years there may be a **succession** of different types of plant communities within a given area, each community replacing an older one as it develops and expands. Plant succession is usually a slow process and thus ordinarily cannot be readily observed, unless one visits the same area at regular intervals through a number of years. The actual causes of succession of communities are many; among them are extensive climatic changes, alterations in topographic features resulting from erosion or deposition of eroded materials, and biotic factors, such as the accumulation of organic matter in soils following leaf fall and decomposition, the destruction of certain community components by virulent parasites, the overgrazing of vegetation by wild or domesticated animals, etc.

The succession of communities may be observed under many conditions in different kinds of environments; for example, along the flood plains or deltas of rivers, where water-borne debris is deposited and

builds up a substratum upon which successive communities may develop; in lakes and ponds which are slowly filled by the growth of peat moss and other mosses and the slow accumulation of organic debris and in which the original aquatic communities are replaced in turn by swamp vegetation and finally by some type of mesophytic community. A long series of community successions is observable upon bare rock surfaces, which are ordinarily first colonized by pioneer lichen communities; the carbon dioxide and possibly other materials excreted by the lichens slowly disintegrate the surface layers of rock and form a substratum upon which xerophytic mosses, ferns, and seed plants are able to grow; with further decomposition of rock and the accumulation of organic materials in crevices, mesophytic species of plants are able to gain a hold and to lead ultimately to a well developed mesophytic community on what was once a bare rock surface.

As environmental factors of a given habitat change, then, various communities appear in succession, until ultimately a relatively stable community becomes established. This relatively permanent community which maintains itself with little change so long as there are no major alterations in the immediate environment is termed the **climax community** of that particular habitat. The climax community of a given area may be regarded as the type of community which is best adapted to that area — that is, which grows better in that particular environment than any other assemblage of plants. Examples of climax vegetations are the deciduous forests of the northeastern United States, the grassland communities of the Great Plains, Douglas fir forests of the Pacific Northwest, and the sagebrush communities of Nevada and Utah.

When a major environmental change occurs which destroys the climax vegetation or throws it out of equilibrium with the factors of the environment, the climax community may be replaced by another type of community which may maintain itself for some time under the changed environmental conditions. If the original conditions which supported the first climax are restored, this earlier climax may invade the newer community, dominate it and establish itself once again as the climax of that region. During forest fires the climax vegetation is destroyed and another type of community usually replaces it, for the conditions which supported the climax (the physical properties of the soil, the humus in the soil, etc.) are no longer present. The newer community may persist for a considerable period of time, during which soil and other conditions gradually return to the state at which they

were when they supported the climax. As the environment which made the climax community possible is restored, the climax community may again appear and establish itself as the dominant, stable vegetation of that area. When yellow pine forests of the Rocky Mountains are burned, for example, the vegetation which gradually appears following the fires is not the same type as that which was burned but consists of some other type of conifers such as lodgepole-pine or of aspens. These plants occupy the burned areas for a time and, as soil conditions and other factors slowly return to those which supported the yellow-pine climax, the climax community is re-established. The destruction of a climax forest by lumbering or by burning usually sets back the succession of communities a number of stages; this succession of communities must then proceed again before the climax vegetation is re-established.

7. PLANT FORMATIONS

A **plant formation** is an aggregation of a number of communities in a region of rather uniform climatic conditions. Thus, a plant formation is a rather large vegetational unit, which is composed of smaller units, the constituent **communities.** In widely separated regions of similar climates, similar plant formations exist, although the species of plants which constitute their communities may be different. For example, the plant formation found in the arid and semi-arid regions of New Mexico and Arizona is very similar to the formation in the arid and semi-arid areas of Western Africa; also, the coniferous forest formation which grows upon the Rocky Mountains of North America is similar in general to that which occurs upon the slopes of the European Alps, although the constituent species in these two widely separated parts of the world are different.

There are two principal groups of plant formations, **terrestrial formations,** which cover the land areas of the earth wherever environmental conditions can support vegetation, and **aquatic formations,** which are composed of communities of plants which inhabit the waters of the earth — lakes, ponds, and oceans. In this chapter, attention will be centered upon the terrestrial formations, since they are more extensive and more varied, and since they are more readily observed by students.

Terrestrial formations are of four general types: **forests, grasslands, deserts,** and **tundras,** which will be described briefly.

Forests are characterized by the presence of trees which are rela-

tively stable and maintain themselves, so long as environmental conditions which support a forest vegetation continue. Forests are of four general types:

1. **Deciduous forests,** which undergo an annual period of leaf fall because of a cold season or a dry season. Example: oak-hickory forests of the eastern United States.

2. **Coniferous forests,** which are composed of evergreen gymnosperms, such as pines, spruces, firs, etc.; these forests ordinarily are exposed at some time in each year to prolonged drought, protracted winter rains, or severe winter cold.

3. **Tropical rain forests,** which grow in regions continuously warm and moist and which are for the most part composed of broad-leaf evergreen tree species. Example: rain-forests of the Amazon Valley in South America.

4. **Winter-rain forests,** which are exposed usually to drought conditions during the summer and to rainfall during the winter. Plants of these forests are usually broad-leaf evergreens. Examples: **sclerophyll** ("hard leaf") forests of Southern California and of portions of the Mediterranean region.

Grasslands are regions in which the climax communities consist principally of grasses. Trees may occur in small groups, particularly along streams, but they form a minor part of the grassland vegetation. Ecologists recognize several types of grasslands, of which the **prairie,** characterized by strong winds, frequent drought, and great temperature extremes in summer and winter, is an example. Much of the native vegetation of Kansas, Nebraska, the Dakotas, Iowa, Illinois and other states in the great central area of the United States consists of grassland communities.

Deserts are regions characterized especially by scanty rainfall and by high temperatures during the greater part of the year. Desert vegetation consists of such xerophytic plants as cacti, agaves, sagebrush, Yuccas, euphorbias, xerophytic grasses and legumes, and various other species of plants. A large part of the vegetation of the Southwestern United States consists of a desert formation.

Tundras are regions of long cold winters and usually scanty rainfall. The soil rarely thaws to a depth of more than a few inches and thus supports only relatively small plants with limited root systems. Tundra formations are found in the sub-arctic regions of Canada and Siberia, for example, and consist of such plants as grasses, sedges, dwarf rhododendrons, gentians, lichens, and mosses. Tundra plants frequently show

Fig. 288. Map of the vegetation regions of North America, by A. G. Vestal, on base map by J. Paul Goode (No. 202. University of Chicago Press). Divisions of Great Basin and desert region after Shreve. The regions of overlap in the eastern states indicate that vegetation-types of more than one region are represented in the same general area. Thus in the Great Lakes area and the eastern mountains both deciduous and coniferous forests are found. In the eastern part of the prairie region (the entire area within the toothed boundary-line), the stippling indicates that deciduous forest occurs, mostly near the streams, while the flat uplands are mostly covered (or were) with grassland vegetation. Similarly in the South Atlantic and Gulf States, deciduous and coniferous trees are found in both uplands and swampy places. In western Wyoming, southeastern Colorado, New Mexico, and northern Arizona, there is a mingling of desert and Great Plains plants which is not indicated in the map. The narrow belt of redwoods along the California coast and the coniferous forests of the mountains in the Great Basin are also not indicated. Oak and pine forests of the highlands of Chiapas and Central America are omitted.

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xerophytic characters because the cold soil retards the rate of water absorption by roots.

The accompanying vegetation map (Figure 288) shows the distribution of the principal plant formations of North America. These formations are:

1. Tundra, extending from Northwestern Alaska into Northeastern Canada. Principal plants: mosses, lichens, grasses, sedges, rhododendrons, Labrador tea.

2. Northern Evergreen Forest, extending from Alaska to Newfoundland, the St. Lawrence Valley, and the higher elevations of the Appalachian Mountains as far south as North Carolina. The winters are long and cold but the summers are moderately warm and the soil thaws to a much greater degree than does tundra soil. The annual rainfall varies from 15 to 40 inches and atmospheric humidity is usually rather high. Among the characteristic plants of this formation are white spruce, balsam fir, white pine, and, less commonly, black spruce and larch.

3. Eastern Deciduous Forest (Figures 289, 290, 291, 292), occupying most of the eastern third of the United States and extending westward along the rivers into the great plains states. The annual precipitation varies from 30 to 50 inches and atmospheric humidity is moderate to high. The winters are cold, but usually rather short, and the summers are often very warm. Among the common plants of this formation are oaks, hickories, maples, elms, walnuts, sycamore, beech, tulip trees, and basswoods.

4. Southeastern Evergreen Forest, extending along the Coastal Plain from New Jersey to eastern Texas and along the Mississippi to northern Arkansas and southern Missouri. Summer temperatures are rather high and the winters are mild, with little or no snow. The annual rainfall varies from 35 to 60 inches and the humidity is generally high. Characteristic plants of this forest are magnolias, some oaks and beech, pines, bald cypress, and sour gums.

5. Tropical Evergreen Forest, covering the southern part of Florida, parts of the islands of the West Indies, and a large portion of southern Mexico and Central America. The annual rainfall varies from 60 to 100 inches and temperatures are high the year round. This formation includes some of the world's most luxuriant vegetation, consisting of numerous broad-leaf evergreen trees, especially members of the legume and palm families, tropical woody vines (lianas), and many epiphytes, among which are ferns, mosses, orchids, and numerous species of the pineapple family.
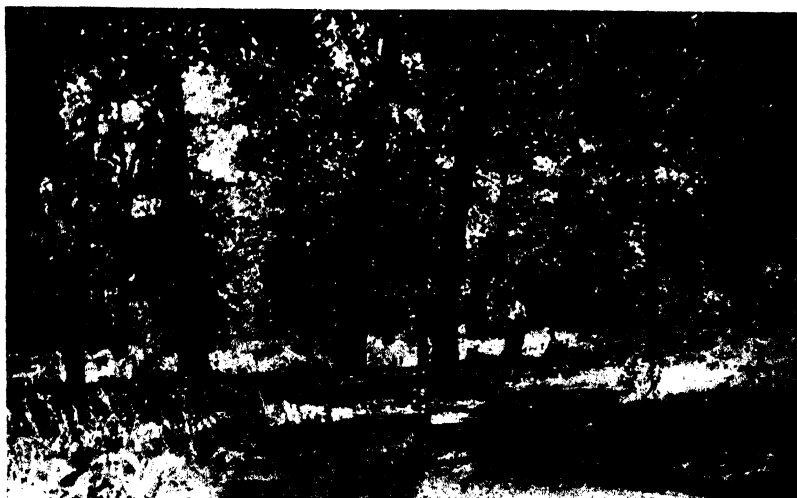
Fig. 289. A Missouri oak-hickory forest, a type of Eastern deciduous forest.

Fig. 290. Eastern deciduous forest formation, showing an oak-hickory community.

Fig. 291. Undergrowth of young trees, shrubs, and herbaceous plants in a moist, eastern deciduous forest. The plants with the large, conspicuous flowers are lady-slipper orchids (*Cypripedium*). Among other plants shown are sedges, grasses, wild strawberries, violets, and button bush.
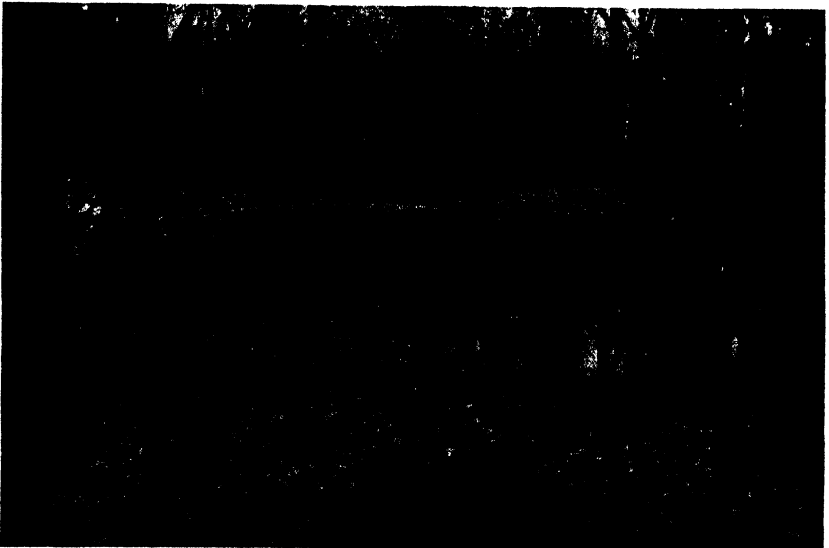
Fig. 292. A deciduous forest in winter. Champaign County, Illinois.
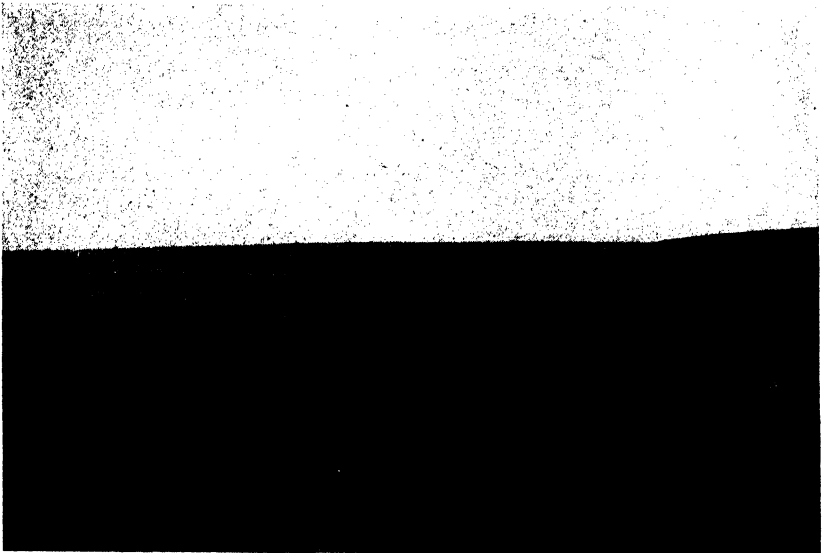
Fig. 293. Manitoba grassland.

6. Grasslands (Figures 293, 294, 295, 296), extending from the western margins of the eastern deciduous forests in Illinois, Indiana, and Missouri, westward to Colorado and Wyoming, and from Texas northward into west central Canada. In this region there are strong winds, high summer temperatures, protracted summer drought, and frequently low winter temperatures. The rainfall varies from 10 to 35 inches and the air often becomes exceedingly dry during late summer and fall. The term "prairie" has been applied to this whole area, and is also used to refer to only the eastern portion of this vast area. The vegetation of the eastern part of the grasslands formation consists principally of tall grasses, such as big blue-stem, turkey-foot grass, Indian grass, and numerous other grasses, and composites such as asters, sunflowers, goldenrods, cone-flowers, and rosin weeds. In the more westerly portions of the grasslands area the extremes of temperature are greater, and the rainfall is less abundant; in this part of the formation grow many short grasses, such as buffalo grass and grama grass, some of which form extensive sods, others of which (bunch grasses) occur in separate, spaced clumps. Also in this western part of the grasslands are many xerophytic or semi-xerophytic herbs, principally members of the legume and composite families.

7. Western Evergreen Forests (Figures 297, 298, 299, 300), extend-
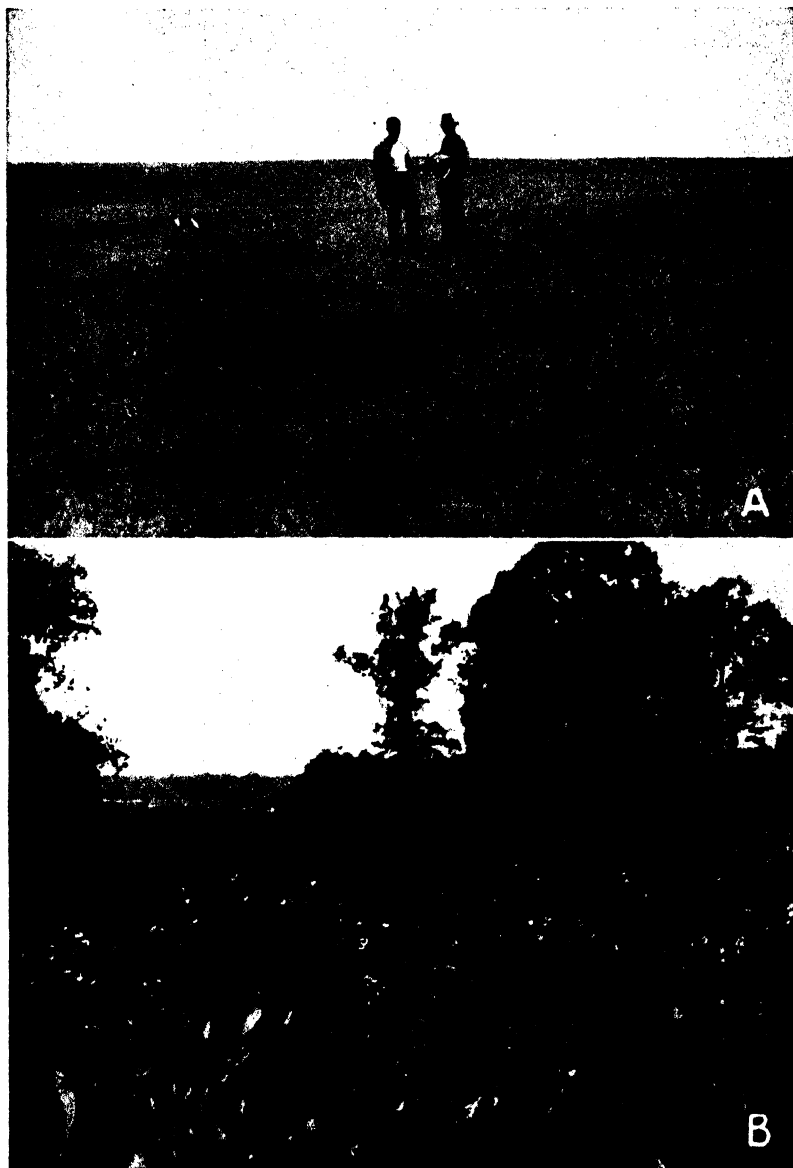
Fig. 294. A. Manitoba grassland. (Photo by H. L. Andrews.)
B. Illinois prairie. The plant with the large leaves is rosin weed. Among the other plants shown are compass plants, grasses, and wild onions. The trees in the background are growing on the banks of a stream. (Photo by V. E. Shelford.)

Fig. 295. Close-up of grassland vegetation, consisting of grasses, sedges, and members of the lily family. Manitoba.
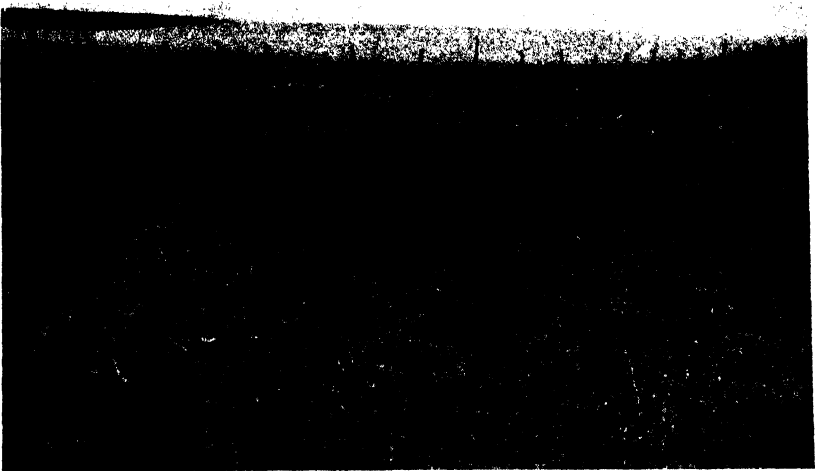
Fig. 296. Overgrazed Colorado grassland, showing broken sod and invading weeds.

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Fig. 297. Coniferous, evergreen forest, consisting largely of firs and spruces. Lake Louise, Canadian Rockies.

ing from Alaska to southern Mexico through the Sierra Nevada Mountains, the Coast Ranges, and the Rocky Mountains. In these vast areas, the dominant plants are coniferous trees. Along the Pacific Coast, in Washington, Oregon and northern California, the forests are temperate rain-forests, growing luxuriantly in a mild, very humid climate and containing some of the world's largest trees, among them Douglas firs, western hemlocks, arbor vitaes, and redwoods, the branches of which are abundantly clad with epiphytic mosses, lichens, and ferns. From Washington north to Alaska, the dominant tree species is the magnificent Sitka spruce. The forests of the southern portion of the Pacific Coast are principally semi-xerophytic, broad-leaf evergreen forests, composed of evergreen oaks and other sclerophyllous trees and shrubs. In the Sierra Nevadas, western yellow pine, sugar pine, incense

Fig. 298. Coniferous forest in the Canadian Rockies. Notice the sharp timberline.

cedar, and Douglas fir are the dominant tree species, with limited stands in California of the world's most majestic tree, the California Big Tree. In the Rocky Mountains the dominant tree is western yellow pine, along with which are several other species of pines, spruces, and firs. In the southern part of the Rocky Mountain area, the evergreen forests consist principally of xerophytic pines and junipers.

8. Southwestern Desert (Figures 301, 302, 303, 304, 305, 306), extending from central Mexico into Southern California, Nevada, Utah, Arizona, New Mexico, western Oregon and Washington, and western Texas. In this region annual rainfall is usually less than 10 inches, the greater part of which usually comes within a few weeks in the fall, winter, or early spring. Atmospheric humidity is low and summer temperatures

Fig. 299. Timberline vegetation, Medicine Bow Mountains, Wyoming. Most of the trees are spruces and firs. The vegetation above timberline consists chiefly of low-growing willows and numerous herbaceous plants such as gentians, primulas, and alpine members of the pink family.
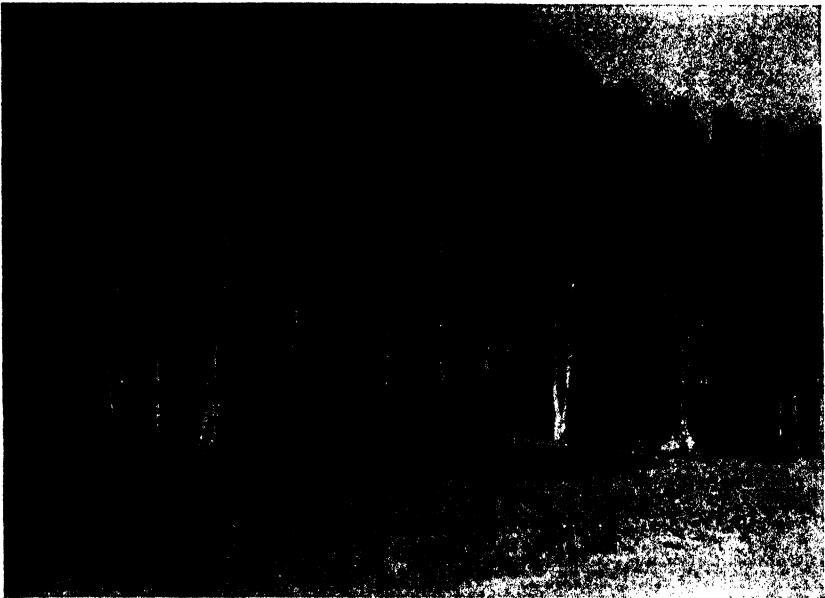
Photo by A. B. Cozzens

Fig. 300. Aspens and spruces in an Arizona mountain forest.

Fig. 301. Desert vegetation in Monument Valley, Utah. The narrow-leaved plants are yuccas.
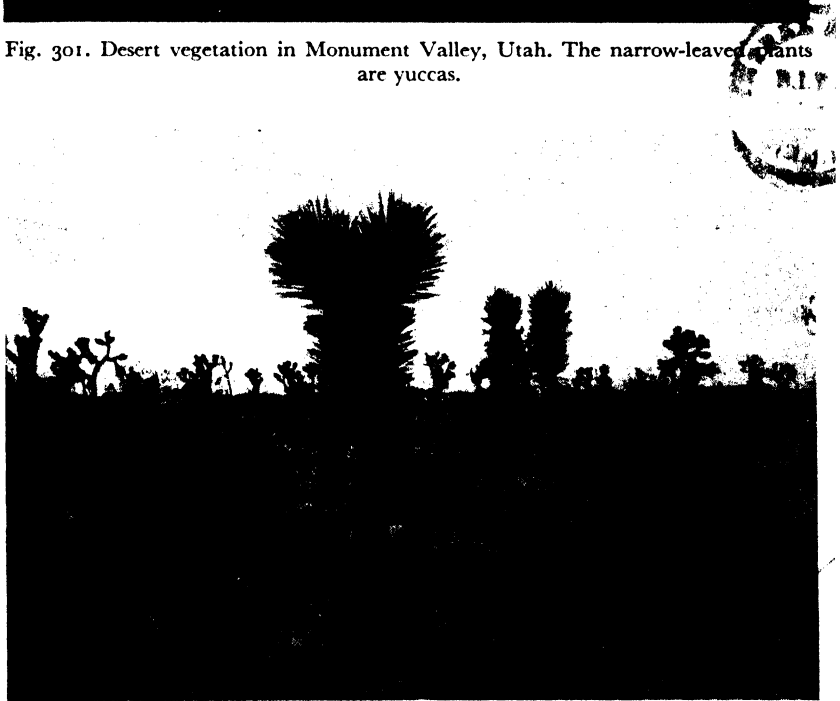
Fig. 302. Joshua trees (*Yucca brevifolia*) and other desert plants in the Mojave desert of California.
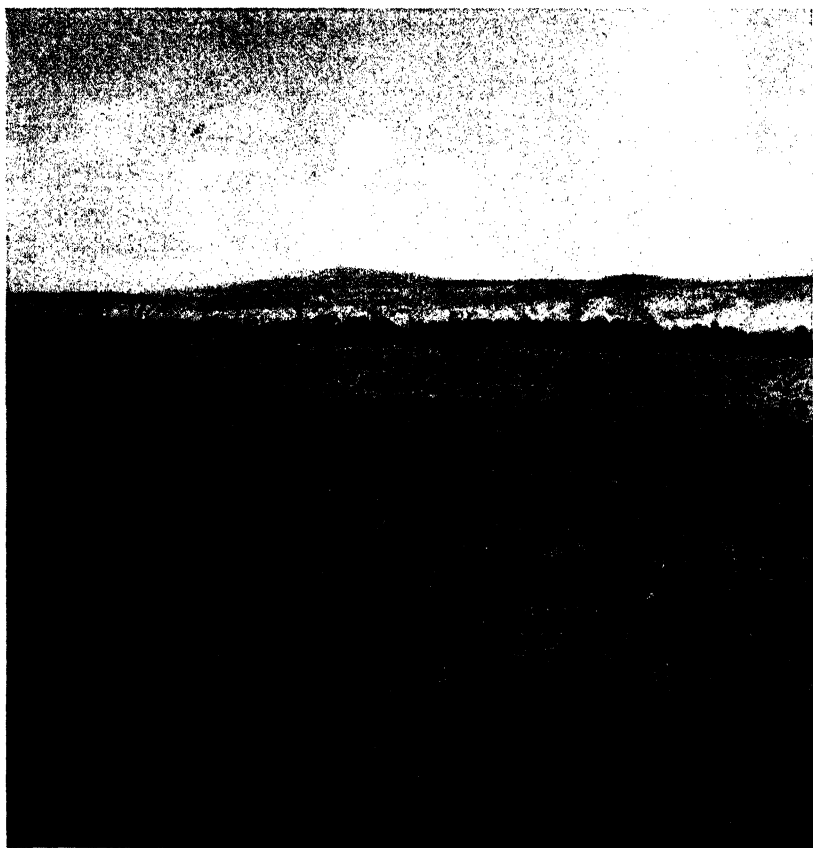
Fig. 303. Utah sage desert, with cottonwood trees along banks of stream in background.

often reach 115° to 120° F. The communities of this desert formation are xerophytic and consist of cacti, thorny desert shrubs, Yuccas, agaves, sagebrush and other woody plants. There are many annuals present which grow quickly and spring into flower within the few weeks of rainfall. At this time the desert is beautiful with the bright flower colors óf these short-lived annuals, the seeds of which remain dormant for many months until the return of the brief rainy season. Also among desert plants are numerous species with well developed bulbs and other types of underground parts which function effectively in the storage of large quantities of water and food. In these desert regions there are occasional streams, along the banks of which cottonwoods and willows commonly grow, as pictured in Figure 303.

Fig. 304. Sagebrush desert in Wyoming. Note the trees in the irrigated meadows, the sparse vegetation on the unirrigated ridge.

SUMMARY

1. The study of the environmental relations of plants is termed plant ecology.

2. The principal factors which influence the distribution of plants are:
   a. Contemporary factors:
      (1) Climatic (atmospheric) factors: light, air temperature, precipitation, winds, etc.
      (2) Edaphic (soil) factors: physical and chemical properties of soils, drainage, soil temperature, etc.
      (3) Biotic factors: relations with other living organisms: saprophytic and parasitic bacteria, higher fungi, and other plants and animals.
   b. Factors of the past.

Fig. 305. Sagebrush-juniper community in a southern Utah desert.

Fig. 306. A characteristic plant of the southwestern desert is the barrel cactus, *Echinocactus polycephalus*.

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Major geological changes, such as glaciation and the recession of glaciers, the subsidence of land masses beneath oceans, the subsequent emergence of such land masses, widespread climatic changes, etc.

3. A plant association or community is a group of plants which live together under the same complex of environmental conditions. Many species are usually present in a community, but communities are usually named after the two or three dominant species of the community.

4. A community is not a static group of organisms but undergoes continuous change. Communities and community components compete with each other, invade each other, etc.

5. During a period of years there may be a succession of communities occupying a given area. Plant succession is usually a relatively slow process and results from extensive climatic changes, alterations of topographic features, local changes such as forest fires, etc.

6. As a result of the succession of communities in a given area, a relatively stable community known as the climax community, becomes established.

7. A plant formation is an aggregation of a number of communities in a region of rather similar climatic conditions. There are two major groups of plant formations: aquatic and terrestrial.

8. The principal types of terrestrial formations are:
    a. Forests.
    b. Grasslands.
    c. Deserts.
    d. Tundras.

9. The principal plant formations of North America are:
    a. Tundra.
    b. Northern evergreen forest.
    c. Eastern deciduous forest.
    d. Southeastern evergreen forest.
    e. Tropical evergreen forest.
    f. Grasslands.
    g. Western evergreen forests.
    h. Southwestern desert.

A Modern Classification of the Plant Kingdom

(Prepared by Dr. O. Tippo)

Sub-kingdom Thallophyta
  Phylum Euglenophyta
    Euglena, etc.
  Phylum Cyanophyta — blue-green algae
    Oscillatoria, etc.
  Phylum Chlorophyta — green algae
    Ulothrix, Oedogonium, etc.
  Phylum   Chrysophyta — yellow-green,   golden-brown   } "Algae"
    algae, and diatoms
    Tribonema, Dinobryon, Navicula, etc.
  Phylum Phaeophyta — brown algae
    Fucus, Laminaria, Ectocarpus, etc.
  Phylum Rhodophyta — red algae
    Nemalion, Geldium, etc.
  Phylum Pyrrophyta — cryptomonads and dinoflagellates
    Peridinium, etc.
  Phylum Schizomycophyta — bacteria
    Bacillus, etc.
  Phylum Myxomycophyta — slime molds
    Fuligo, Stemonites, etc.
  Phylum Eumycophyta — true fungi   } "Fungi"
    Class Phycomycetes — algal fungi
    Class Ascomycetes — sac fungi
    Class Basidiomycetes — club fungi
      (Fungi Imperfecti) — imperfect fungi
Sub-kingdom Embryophyta
  Phylum Bryophyta (Atracheata) — mosses and liverworts
    Class Hepaticae — liverworts
    Class Musci — mosses
  Phylum Tracheophyta (Tracheata) — plants with vascular tissues

Sub-phylum Psilopsida
  Class Psilophytinae
    *Order Psilophytales
      Rhynia, Hornea, Asteroxylon, Psilophyton, etc.
    Order Psilotales
      Psilotum and Tmesipteris
Sub-phylum Lycopsida
  Class Lycopodineae
    Order Lycopodiales — club-mosses
      Lycopodium and Phylloglossum
    Order Selaginellales — small club-mosses
      Selaginella
    *Order Lepidodendrales — lepidodendrids or giant club-mosses
      Lepidodendron, Stigmaria, Lepidostrobus, Sigillaria, Lepidocarpon, etc.
    *Order Pleuromeiales
      Pleuromeia
    Order Isoetales — quillworts
      Isoetes
Sub-phylum Sphenopsida
  Class Equisetineae
    *Order Hyeniales
      Hyenia
    *Order Sphenophyllales
      Sphenophyllum, Cheirostrobus, etc.
    Order Equisetales — horsetails
      Equisetum, Calamites, etc.
Sub-phylum Pteropsida
  Class Filicinae — ferns
    *Order Coenopteridales
      Botryopteris, etc.
    Order Ophioglossales — adder's tongue ferns
      Ophioglossum, Botrychium, Helminthostachys
    Order Marattiales — marattiaceous ferns
      Marattia
    Order Filicales — "true" ferns
      Polypodium, Osmunda, Gleichenia, Salvinia, Marsilea, Schizaea, Hymenophyllum, Azolla, Cyathea, Dicksonia, Dennstaedtia, Adiantum, Pteridium, Pteris
  Class Gymnospermae
    Sub-class Archaeogymnospermae

* Known only as fossils; no living representatives.

    *Order Cycadofilicales (Pteridospermae) — "seed-ferns"
      Lyginodendron, Heterangium, etc.
    *Order Bennettitales
      Bennettites, Cycadeoidea, Williamsonia, Wielandella, etc.
    Order Cycadales
      Zamia, Cycas, etc.
    *Order Cordiatales
      Cordaites, etc.
    Order Ginkgoales
      Ginkgo
  Sub-class Metagymnospermae
    Order Coniferales
      Pinus, Taxus, etc.
    Order Gnetales
      Gnetum, Ephedra, Welwitschia
Class Angiospermae — "flowering plants"
  Sub-class Dicotyledoneae
    Cohort Archichlamydeae (Choripetalae) — "petals absent
      or separate"
    Order Magnoliales (Ranales), etc.
    Cohort Metachlamydeae (Sympetalae) — "petals fused"
  Sub-class Monocotyledoneae

* Known only as fossils; no living representatives.

Glossary

All technical terms used in the text are included in the glossary. The derivations of all words originating from languages other than Anglo-Saxon or Old English are indicated in accordance with the abbreviations following this paragraph. In the case of a few unusual or especially interesting words, Anglo-Saxon and Old English origins are indicated.

Abbreviations:

Ar. — Arabic	Gr. — Greek	OF. — Old French
AS. — Anglo-Saxon	L. — Latin	Sw. — Swedish
Fr. — French	ME. — Middle English	

ABSCISSION (L. *abscissus* — cut off): separation of leaves and other plant parts by the disorganization of an abscission layer.

ABSCISSION LAYER (L. *abscissus* — cut off): separation zone of thin-walled cells formed across the base of a petiole.

ACCESSORY FRUIT (L. *accedere* — approach): a structure consisting of a true fruit (matured ovary), plus other parts, such as calyx or receptacle.

ACHENE: (Gr. *achaines* — with a single prong): a simple, dry, one-seeded, indehiscent fruit, with distinct seed coat and fruit wall.

ACTIVE ABSORPTION: (L. *absorbere* — suck in): the intake of materials by a cell usually against a concentration gradient and as a result of the expenditure of energy by the absorbing cell.

ADAPTATION (L. *ad* — to, and *aptere* — to fit): adjustment to environmental conditions.

ADSORPTION (L. *ad* — to, and *sorbere* — suck in): the adhesion in very thin layers of a substance to the surface of a solid body with which it is in contact; the particles which adsorb other materials are chiefly colloidal.

ADVENTITIOUS (L. *adventitius* — foreign): arising from an unusual place.

ADVENTITIOUS BUD: a bud which develops in some other place than the axils of leaves.

ADVENTITIOUS ROOTS: roots which do not arise from a primary root or one of its branches but which arise from leaves, stems, etc.

AECIOSPORE (Gr. *aikia* — injury, and Gr. *spora* — spore, seed): a rust spore, produced in an aecium.

AECIUM (Gr. *aikia*): a cup-shaped structure within which rust spores are produced.

AERIAL STEM (Gr. *aerios* — air, mist): a stem which grows above the soil.

AEROBIC RESPIRATION (Gr. *aerios* — air, mist, and L. *re* — again, *spiro* — breath): respiration in the presence of free, gaseous oxygen.

AGGREGATE FRUIT (L. *aggregare* — collect): a cluster of fruits developed from the ovaries of a single flower.

AGRONOMY (Gr. *agros* — field, and Gr. *nemo* — graze): the science of field crops.

ALGAE (L. *alga* — seaweed): the chlorophyllous thallophytes.

ALKALOID (Ar. *al-qili* — ashes of the saltwort plant): a nitrogenous organic substance of alkaline (basic reaction).

ALTERNATE (L. *alternus* — by turns): describing the condition in which a single leaf or bud occurs at a node.

ALTERNATION OF GENERATIONS (L. *alternus* — by turns, and L. *genero* — bring to life): the alternation of a spore-producing phase and a gamete-producing phase in the life-cycle of a plant.

AMINO ACIDS (L. *Ammon* — referring to the discovery of sal ammoniac in camel's dung near the Temple of Jupiter Ammon, and L. *acidus* — sour): organic nitrogenous acids from which protein molecules are synthesized.

AMMONIFICATION (L. *Ammon* — see amino acid, and L. *facio* — to make): formation of ammonia following the decomposition of amino acids.

AMMONIFYING BACTERIA (L. *Ammon* plus L. *facio* — see ammonification; Gr. *bacterion* — stick, referring to rod-shaped bacteria): bacteria which cause ammonification.

AMYLASE (Gr. *amylon* — starch): an enzyme which hydrolyzes starch to maltose.

ANABOLISM (Gr. *ana* — up, and Gr. *ballo* — throw or put): constructive metabolism.

ANAEROBIC RESPIRATION (see aerobic respiration): respiration in the absence of free oxygen, or in the presence of reduced concentrations of free oxygen.

ANAPHASE (Gr. *ana* — up, and Gr. *phasis* — appearance): a stage in mitosis in which the halves of the divided chromosomes move toward opposite ends of the spindle.

ANATOMY (Gr. *ana* — up, and Gr. *tome* — cutting): the phase of morphology which treats of the detailed internal structure of organisms.

ANNUAL (L. *annus* — year): a plant which completes its life-cycle and dies within one year.

ANNUAL RING (L. *annus* — year): the layer of xylem (wood) formed by one year's growth of the cambium.

ANNULUS (L. *annulus* — a ring): a row of specialized cells in the wall of a fern sporangium.

ANTHER (Gr. *anthos* — flower): pollen-bearing part of a stamen.

ANTHERIDIUM (Gr. *anthos* — flower, and Gr. *–idion*, a diminutive ending): a structure which produces sperms.

ANTHOCYANIN (Gr. *anthos* — flower, and Gr. *kyanos* — dark blue): blue, red, or purple pigment.

ANTIBODY (Gr. *anti* — against, and AS. *bodig* — organized mass or substance): a substance or body in the tissues or blood of an organism which inactivates or destroys foreign bodies, such as bacterial poisons.

APICAL GROWTH (L. *apex* — summit): growth occurring at the tip or apex of an organ.

ARCHEGONIUM (Gr. *archaios* — primitive, and Gr. *gonos* — offspring, reproduction): a multicellular egg-producing structure in plants.

ASCOMYCETES (Gr. *askos* — bag, and Gr. *mykes* — fungus): one of the classes of fungi, characterized by the formation of asci and ascospores; known commonly as the sac-fungi.

ASCOSPORE (Gr. *askos* — bag, and Gr. *spora* — spore, seed): a spore produced by the ascomycetes in an ascus.

ASCUS (Gr. *askos* — sac): a sac-like structure within which ascospores are formed.

ASEXUAL (L. *sexus* — sex): referring to any type of reproduction which does not involve the union of sex-cells (gametes).

ASSIMILATION (L. *assimilare* — to make like): the transformation of foods into living protoplasm.

AUTOTROPHIC (Gr. *auto* — self, and Gr. *trophe* — food): referring to a plant which is able to manufacture its own food.

AUXINS (Gr. *auxe* — growth): growth-regulating substances (plant hormones).

AXIL (L. *axilla* — armpit): the upper angle between a twig or a leaf-stalk and the axis from which it grows.

AXILLARY BUD (L. *axilla* — armpit): a bud borne in the axil of a leaf.

BACILLUS (L. *baculum* — stick): a rod-shaped bacterium.

BACTERIA (Gr. *bakterion* — stick): the members of the morphologically-simplest group of fungi.

BACTERIOLOGY (Gr. *bakterion* — stick, and Gr. *logos* — discourse, account): the science of bacteria.

BARK (Sw. *bark* — rind): the aggregation of tissues outside the cambium, chiefly of woody stems.

BASIDIOMYCETES (Gr. *basis* — pedestal, and Gr. *mykes* — fungi): a class of fungi in which spores are produced on short stalks growing from a club-shaped structure, the basidium; known commonly as the club-fungi.

BASIDIOSPORES (Gr. *basis* — pedestal, and Gr. *spora* — seed, spore): the spores of the basidiomycetes produced in basidia.

BASIDIUM (Gr. *basis* — pedestal): the characteristic club-shaped spore-producing structure of the basidiomycetes.

BERRY (AS. *berige* — berry): a simple fruit, the entire pericarp of which is fleshy.

BIENNIAL (L. *biennium* — a two-year period): a plant which produces seed during its second year of life and then dies.

BILATERAL SYMMETRY (L. *bis* — two, and L. *latus* — side; Gr. *sym* — together, and Gr. *metron* — measure): the condition of having distinct and similar right and left sides, as in the flowers of a pea or snap-dragon.

BLADE (AS. *blaed* — leaf): the expanded portion of a leaf.

BRACT (L. *bractea* — a thin plate of precious metal): a leaf from the axil of which a flower or inflorescence arises.

BRYOPHYTA (Gr. *bryon* — moss, and Gr. *phyton* — plants): a division of the plant king-dom comprising the liverworts and mosses.

BUD (ME. *budde* — bud): on a stem, a terminal or axillary swelling consisting of a small mass of meristematic tissue, covered wholly or in part by overlapping leaves.

BUD-SCALE (ME. *budde* — bud, and AS. *scale* — bowl): a specialized protective leaf of a bud.

BUD SCAR (ME. *budde* — bud, and Gr. *eschara* — fireplace, scab): a scar left on a twig by the falling away of a bud or bud scales.

BULB (Gr. *bolbos* — an enlarged root): a short, usually globose underground stem, bearing many fleshy, food-storing scale-leaves.

BUNDLE SCARS: scars left in leaf scars at time of leaf fall by breaking of vascular bundles passing from stem into petiole.

CALYX (Gr. *kalyx* — cup): collective term for the sepals of a flower.

CAMBIUM (L. *cambium* — exchange): layer of meristematic cells between the xylem and phloem tissues.

CAPILLARY WATER (L. *capillus* — hair): water retained in the spaces among small particles after drainage.

CAPSULE (L. *capsa* — box): a simple, dehiscent, dry fruit composed of two or more carpels.

CARBOHYDRATE (L. *carbo* — coal, and Gr. *hydor* — water): a group of foods composed of carbon, hydrogen, and oxygen, with the hydrogen and oxygen in the ratio of 2 to 1.

CARBONIFEROUS PERIOD (L. *carbo* — coal, and L. *fero* — bear): a period of the Paleozoic era, characterized by the formation of great coal beds.

CARNIVOROUS (L. *caro* — flesh, and L. *voro* — devour): meat-eating.

CAROTIN (L. *carota* — carrot): a reddish-orange pigment found in plant cells.

CARPEL (Gr. *karpos* — fruit): a floral organ which bears ovules.

CARUNCLE (L. *caruncula* — fleshy growth): a spongy structure at one end of a castor-bean seed.

CARYOPSIS (Gr. *karyon* — nut, and Gr. *opsis* — appearance): a fruit characteristic of grasses; the fruit is dry, one-seeded, indehiscent, with the seed coat and pericarp completely united.

CATABOLISM (Gr. *kata* — down, and Gr. *ballo* — throw): destructive metabolism.

CATALYST (Gr. *kata* — down, and Gr. *luo* — dissolve): a substance which regulates the speed of a chemical reaction without being used up in the reaction.

CATKIN ("cat" and diminutive "kin"): a spike-inflorescence bearing staminate or pistillate apetalous flowers; the spike falls as a whole.

CELL (L. *cella* — small room): the unit of structure of plants and animals; the essential feature of a cell is its living protoplasm, surrounded in plant cells by a wall.

CELL-DIVISION (L. *cella* — little room, and L. *divido* — divide): a process whereby cells reproduce.

CELL SAP (L. *cella* — small room): the liquid in the vacuoles of plant cells.

CELL THEORY (L. *cella* — small room): a theory which states that the structural and functional units of living organisms are cells and that the development of organisms proceeds from the formation of new cells.

CELLULOSE (L. *cella* — a small room): a complex carbohydrate forming the major part of the cell walls of most plants.

CHEMOSYNTHESIS (Gr. *chemeia* — chemistry, and Gr. *syn* — together, and Gr. *thesis* — setting, arrangement): a process of food-manufacture, utilizing energy derived from chemical reactions, such as the oxidation of sulfur, ammonia, etc.

CHEMOTROPISM (Gr. *chemeia* — chemistry, and Gr. *trope* — turn): a growth movement induced by a chemical stimulus.

CHLORENCHYMA (Gr. *chloros* — green, and Gr. *chymos* — juice): tissues containing chlorophyll.

CHLOROPHYCEAE (Gr. *chloros* — green, and Gr. *phykos* — seaweed): the green algae.

CHLOROPHYLL (Gr. *chloros* — green, and Gr. *phyllon* — leaf): a green pigment found chiefly in chloroplasts and involved in photosynthesis.

CHLOROPLAST(ID) (Gr. *chloros* — green, and Gr. *plastos* — formed): specialized cytoplasmic structures containing chlorophyll.

CHLOROSIS (Gr. *chloros* — green, and Gr. *osis* — diseased state): failure of chlorophyll development because of nutritional disturbance, such as lack of iron or magnesium, or because of disease.

CHONDRIOSOMES (Gr. *chondros* — granular, and Gr. *soma* — material, body): small, rod-shaped cytoplasmic bodies found in many types of cells. Same as mitochondria.

CHROMATIN (Gr. *chroma* — color): deeply-staining nuclear material of which the hereditary determiners are composed.

CHROMOPLAST(ID) (Gr. *chroma* — color, and Gr. *plastos* — formed): yellowish or red cytoplasmic body containing carotin and xanthophyll.

CHROMOSOMES (Gr. *chroma* — color, and Gr. *soma* — body): nuclear bodies of definite structure and number formed from chromatin during mitosis.

CILIA (L. *cilium* — eyelash): protoplasmic extrusions which propel certain types of unicellular organisms, gametes, and zoospores through water.

CLASS: one of the sub-groups of a division of the plant kingdom.

CLUB FUNGI (L. *fungus* — mushroom): the basidiomycetes.

CLUB-MOSSES: a class of the pteridophytes.

COCCUS (Gr. *kokkos* — berry): a spherical bacterium.

COLLENCHYMA (Gr. *kolla* — glue, and Gr. *chymos* — juice): a strengthening tissue, composed of cells with walls usually thickened at the angles of the walls.

COLLOID (Gr. *kolla* — glue, and Gr. *eidos* — form): a state of subdivision or dispersion in which the particles of the dispersed substance are of super-molecular size and in which the particles do not diffuse (or diffuse very slowly) through membranes.

COLONY (L. *colo* — cultivate, dwell): a group of similar organisms living together in close association; more specifically, a group of associated unicellular organisms among which there are no structural differences and no division of labor.

COMPANION CELLS (L. *cum* — together, L. *panis* — bread, and L. *cella* — small room): elongated cells adjoining sieve tubes in phloem tissue.

COMPLETE FLOWER (L. *flos* — flower): a flower which bears 4 types of floral organs — sepals, petals, stamens, and carpels.

COMPOUND LEAF: a leaf the blade of which is subdivided into several distinct parts.

COMPOUND PISTIL: a pistil composed of two or more partially or wholly fused carpels.

CONCEPTACLE (L. *concipere* — receive): in certain thallophytes, a cavity within which the antheridia or oogonia are produced.

CONE (Gr. *konos* — a pine cone): a reproductive branch bearing sporophylls.

CONIFERS (Gr. *konos* — pine cone, and L. *fero* — carry): a group of cone-bearing trees, such as pines, in the gymnosperms.

CONJUGATION (L. *cum* — with, and L. *jugum* — yoke): a type of isogamous sexual reproduction.

CONVERGENT EVOLUTION (L. *cum* — with, L. *verto* — turn, and Gr. *genea* — birth): evolution of unrelated or distantly related groups of organisms along similar lines.

CORK (L. *quercus* — oak): a suberized tissue formed on the stem and root surfaces (sometimes also on other parts) chiefly of woody plants from the cork cambium.

CORK CAMBIUM (L. *quercus* — oak; L. *cambium* — exchange): a meristematic tissue which is formed in woody stems usually from certain cells of the cortex and which produces cork cells.

CORM (Gr. *kormos* — tree trunk): a short, often globose, vertical underground stem which stores food; differs from a bulb in that the latter consists chiefly of fleshy storage leaves growing from a small stem, whereas a corm is chiefly stem tissue.

COROLLA (L. *corolla* — diminutive of *corona* — crown): collectively, the petals of a flower.

CORRELATION (L. *cum* — with, and L. *relatus* — reported, referred): the mutual interaction of plant parts and processes.

CORTEX (L. *cortex* — bark): tissues lying between the epidermis and endodermis of a stem or root.

COTYLEDON (Gr. *kotyle* — cup): a food-digesting and food-storing part of an embryo; also known as seed leaf.

CROSS-POLLINATION (L. *pollen* — flower): the transfer of pollen from a stamen to the stigma of a flower on another plant.

CRUSTOSE LICHENS (L. *crusta* — crust; Gr. *leichen* — tree moss): lichens which grow closely appressed to the substratum and have a crusty appearance.

CUTICLE (L. *cutis* — skin): waxy layer formed on outer walls of epidermal cells.

CUTIN (L. *cutis* — skin): waxy substance which is very impermeable to water.

CUTINIZATION (L. *cutis* — skin): process of impregnating cell walls with cutin.

CYCADS (Gr. *kykas* — coco palm): a small group of gymnosperms with palm-like leaves and conspicuous cones.

CYTOLOGY (Gr. *kytos* — hollow, and Gr. *logos* — discourse): the science of cell structure and function.

CYTOPLASM (Gr. *kytos* — hollow, and Gr. *plasma* — form): all the protoplasm in a cell outside the nucleus.

CYTOPLASMIC MEMBRANE (see cytoplasm; L. *membrana* — skin): membranes on the surface of cytoplasm and between cytoplasm and vacuoles.

DAUGHTER CELL: a cell newly formed as a result of the division of a parent cell (mother cell).

DECIDUOUS (L. *deciduus* — falling): referring to perennial plants which lose their leaves in the autumn, and to the falling of other parts, such as flower parts, etc.

DEHISCENT (L. *dehiscere* — to split open): splitting along definite lines at maturity.

DENITRIFICATION (L. *de* — down, off; Gr. *nitron* — saltpeter; L. *facio* — make): conversion of nitrogenous compounds in the soil into gaseous nitrogen.

DENITRIFYING BACTERIA: bacteria which bring about denitrification in the soil.

DIATOMACEOUS EARTH: a type of sedimentary deposit consisting of the dead bodies of diatoms.

DIATOMS (Gr. *dia* — through, across; Gr. *tomos* — cut): a group of unicellular algae, with siliceous walls.

DICOTYLEDONS (Gr. *dis* — two; Gr. *kotyle* — cup): a group of angiosperms with embryos bearing two cotyledons.

DIFFERENTIALLY PERMEABLE: referring to membranes which allow certain substances to pass through and which retard or prevent the passage of others.

DIFFERENTIATION (L. *differere* — carry apart, to be different): modification of tissues or organs for the performance of different functions.

DIFFUSE-POROUS WOOD (L. *diffusus* — poured out, dispersed; Gr. *poros* — opening; AS. *wudu* — wood, tree): a type of wood in which the vessels are more or less uniformly distributed throughout each annual ring.

DIFFUSE (FIBROUS) ROOT SYSTEM (L. *diffusus* — poured out): a root system in which there are numerous main roots of approximately equal size.

DIFFUSION (L. *diffusus* — poured out): the spreading of a substance throughout available space from high to low concentrations, as a result of molecular motion.

DIGESTION (L. *digerere* — separate, dissolve): the transformation of insoluble or complex substances into soluble or simpler substances, through the action of enzymes.

DIHYBRID CROSS (Gr. *dis* — two, L. *hybrida* — mongrel): a cross between organisms differing in two characters.

DIOECIOUS (Gr. *dis* — two, and Gr. *oikos* — house): having the male and female organs or staminate and pistillate flowers on separate plants.

DIPLOID (Gr. *diploos* — double): referring to the double chromosome number, characteristic of the sporophyte generation in plants.

DISBUDDING (L. *dis* — apart, ME. *budde* — bud): the removal of buds from a plant to control the branching or to produce larger flowers from the remaining buds.

DISEASE (L. *dis* — apart, asunder, and OF. *aise* — ease): an abnormal condition of sufficient duration to produce marked derangements in the structure or activities of an organism or its parts.

DIVISION (L. *divido* — divide): one of the four major groups of the plant kingdom.

DOMINANCE (L. *dominor* — rule): a condition in which one of a pair of contrasting characters hides or masks the other character when both are present in an individual.

DORMANCY (L. *dormio* — sleep): a period of reduced physiological activity occurring in seeds, buds, etc., resting period.

DRUPE (Gr. *druppa* — over-ripe olive): a simple fleshy fruit in which the endocarp (inner wall of ovary) becomes hard and stony, and encloses one or two seeds.

ECOLOGY (Gr. *oikos* — home, and Gr. *logos* — discourse): the study of plants in relation to their environments.

EGG (AS. *aeg* — egg): female gamete.

EMBRYO (Gr. *embryon* — embryo): a young sporophytic plant, before the beginning of its rapid growth; the "germ" of a seed.

ENDOCARP (Gr. *endon* — within, and Gr. *karpos* — fruit): inner layer of fruit wall.

ENDODERMIS (Gr. *endon* — within, and Gr. *derma* — skin): a layer of cells just inside the cortex; most conspicuous in roots.

ENDOSPERM (Gr. *endon* — within, Gr. *sperma* — seed): a food storage tissue in seeds; in gymnosperms, the endosperm is a part of the female gametophyte and is haploid; in angiosperms, it results from the fusion of a sperm with two polar nuclei of the embryo sac and is triploid.

ENZYME (Gr. *en* — in, Gr. *zyme* — yeast): an organic catalyst, manufactured by living protoplasm and controlling digestion and other physiological processes.

EPICOTYL (Gr. *epi* — upon, over, and Gr. *kotyle* — cup): the portion of an embryo above the attachment of the cotyledons.

EPIDERMIS (Gr. *epi* — upon, and Gr. *derma* — skin): the surface layer of cells of leaves and other young or short-lived plant parts.

EPIGYNY (Gr. *epi* — upon, and Gr. *gyne* — female): a condition in which the ovary is embedded in the receptacle, so that the other flower parts seem to arise from the top of the ovary.

ETIOLATION (Fr. *étioler* — blanch): a condition involving abnormal stem elongation, failure of normal leaf development, and absence of chlorophyll, and characterizing plants growing in the absence of light.

EVOLUTION (L. *evolutio* — unroll): the history of development of a race or species or larger biological group; phylogeny.

EXCITATION (L. *excitare* — to rouse): the irritation or protoplasmic disturbance produced by a stimulus.

EXOCARP (Gr. *exo* — outside, and Gr. *karpos* — fruit): outermost layer of a fruit wall.

EYESPOT: a small, light-sensitive, pigmented structure present in certain algae.

FAMILY: a taxonomic category ranking between genera and an order.

FAT: a kind of food, which is insoluble in water and is made up of carbon, hydrogen, and oxygen, with proportionately less oxygen than carbohydrates contain.

FERMENTATION (L. *fermentum* — yeast): anaerobic respiration; decomposition of organic substances by living organisms in the absence of free oxygen or in the presence of reduced concentrations of free oxygen.

FERNS: the largest group of living pteridophytes.

FERTILIZATION (L. *fertilis* — producing, fertile): the essential feature of sexual reproduction — the fusion of one gamete with another.

FIBER (L. *fibra* — fiber): an elongated, tapering, thick-walled, strengthening cell, occurring in various parts of plant bodies.

FILAMENT (L. *filum* — thread): the stalk of a stamen, with an anther at its apex; also, a thread-like row of cells.

FISSION (L. *fissus* — split): asexual reproduction, in which a one-celled organism divides into two one-celled organisms.

FLAGELLATES (L. *flagellum* — whip): a group of primitive unicellular organisms of doubtful relationship; the green flagellates are often classed as algae.

FLAGELLUM (L. *flagellum* — whip): a protoplasmic extrusion the movements of which propel unicellular organisms, zoospores, etc. through water.

FLORICULTURE (L. *flos* — flower, and L. *colere* — till, cultivate): the study of the cultivation of ornamental flowering plants.

FLOWER BUD: a bud which grows into a flower.

FOLIOSE LICHENS (L. *folium* — leaf, and Gr. *leichen* — tree-moss): flattened, somewhat broadened lichens of leaf-like appearance.

FOLLICLE (L. *follis* — bag): a simple, dry, dehiscent fruit, producing several to numerous seeds and composed of one carpel, which splits along one seam.

FOOD: an organic substance which furnishes energy for vital processes or which is transformed into living protoplasm and cell walls.

FOOT: in bryophytes and pteridophytes, a portion of a young sporophyte which attaches the sporophyte to the gametophyte and often absorbs food from the latter.

FOSSIL (L. *fossus* — dug): an impression or trace of a plant in the earth's crust.

FRUIT: a matured ovary.

FRUTICOSE LICHENS (L. *frutex* — shrub, and Gr. *leichen* — tree-moss): a branching, shrub-like lichen.

FUNGI (L. *fungus* — mushroom): non-chlorophyllous plants constituting a subdivision of thallophytes.

FUNICULUS (L. *funis* — cord): stalk which attaches an ovule to the ovary wall.

GAMETANGIUM (Gr. *gametes* — spouse, and Gr. *angos* — vessel): a structure bearing gametes.

GAMETES (Gr. *gametes* — spouse): a sex cell, which fuses with another gamete in sexual reproduction.

GAMETOPHYTE (Gr. *gametes* — spouse, and Gr. *phyton* — plant): the sexual, or gamete-producing generation, characterized by the haploid chromosome number.

GEL (L. *gelo* — freeze): jelly-like colloidal system.

GEMMA (L. *gemma* — bud): an asexual, or vegetation outgrowth of a parent body, capable of growing into a new individual. Gemmae occur in bryophytes and pteridophytes.

GENE (Gr. *genesis* — origin): a hereditary determiner, located on a chromosome.

GENERATIVE NUCLEUS (Gr. *genesis* — origin, and L. *nux* — nut): the nucleus in a pollen tube which upon cell division forms two sperms.

GENETICS (Gr. *genesis* — origin): the science of heredity.

GENOTYPE (Gr. *genesis* — origin, and Gr. *typos* — model): the genetic constitution of an organism; a type determined by genes.

GENUS (L. *genus* — race, kind): a group of closely related species.

GEOTROPISM (Gr. *ge* — earth, and Gr. *trope* — turn): a growth movement induced by gravitational stimulus.

GERMINATION (L. *germen* — sprig): the beginning of growth of a seed, spore, bud, or other structure.

GIRDLING: the removal of a ring of bark from a portion of a stem.

GLUCOSE (Gr. *glykus* — sweet): grape sugar, or dextrose.

GRAFTING (Gr. *graphion* — pencil, stylus): the joining of two plant parts, usually stems, so that their tissues grow together.

GRAIN (L. *granum* — grain): the fruit of a grass, or more specifically of a cereal grass.

GRAVITATIONAL WATER (L. *gravis* — heavy): water which moves downward through soil as a result of the earth's gravitational force upon it.

GUARD CELLS: paired chlorophyllous-epidermal cells which enclose stomata.

GUM: colloidal, mucilaginous, water-soluble plant exudations, with numerous economic uses.

GUTTATION (L. *gutta* — drop of liquid): the exudation of liquid water from plants.

GYMNOSPERMS (Gr. *gymnos* — naked, and Gr. *sperma* — seed): a subdivision of spermatophytes, with seeds borne on the surfaces of cone-scales.

HALOPHYTE (Gr. *hals* — salt, and Gr. *phyton* — plant): a plant which grows in alkali soils or salt marshes.

HAPLOID (Gr. *haploos* — single): referring to the single chromosome number, characteristic of the gametophyte generation.

HARDWOOD: the wood of angiosperms.

HAUSTORIUM (L. *haurire* — draw up, drink): in parasitic plants, sucker-like structures which penetrate host tissues and absorb food from them.

HEAD: a type of inflorescence, in which numerous small flowers are crowded upon a usually disc-shaped common receptacle.

HEARTWOOD: the inner, dead, non-conducting, usually dark-colored wood of a tree or shrub.

HERB (L. *herba* — grass): a plant which does not develop much woody tissue and which thus remains soft and succulent.

HERBACEOUS PLANT: herb.

HERBALS (L. *herba* — grass): medieval books picturing and describing plants, their uses and mythology, etc.

HERBIVOROUS (L. *herba* — grass, and L. *voro* — eat): plant-eating.

HEREDITY (L. *heres* — heir): the resemblance between parents and offspring.

HETEROECISM (Gr. *heteros* — different, and Gr. *oikos* — house): in rusts, the completion of the life cycle upon two kinds of host plants.

HETEROGAMETES (Gr. *heteros* — different, and Gr. *gametes* — spouse): gametes which differ in size, structure, and behavior.

HETEROGAMY (Gr. *heteros* — different, and Gr. *gamos* — marriage): sexual reproduction by gametes differing in size, structure, and behavior.

HETEROTROPHIC (Gr. *heteros* — different, and Gr. *trophe* — food): referring to organisms which are unable to make their food and which are thus parasitic or saprophytic.

HETEROZYGOUS (Gr. *heteros* — different, and Gr. *zygon* — yoke): refers to an organism with differing paired genes — that is, an organism which does not breed true.

HILUM (L. *hilum* — a trifle): scar on a seed coat, marking the place of attachment of the seed stalk to the seed.

HISTOLOGY (Gr. *histos* — web, tissue): the microscopic study of tissues.

HOLDFASTS: basal portions of thalli which anchor them to solid objects in the water.

HOMOLOGOUS CHROMOSOMES (Gr. *homo* — same, Gr. *logos* — history, discourse; Gr. *chroma* — color, Gr. *soma* — body): the members of a chromosome pair.

HOMOZYGOUS (Gr. *homos* — same, Gr. *zygon* — yoke): refers to an organism with similar paired genes — that is, an organism which will breed true for a given pair of genes.

HORMONE (Gr. *hormao* — excite): a chemical agent produced in one part of a plant which controls or influences a process in another part of a plant.

HORSE-TAILS: a small group of reed-like pteridophytes.

HORTICULTURE (L. *hortus* — garden, and L. *cultra* — cultivation): the cultivation of orchard and garden plants.

568 GLOSSARY

HYBRID (L. *hybrida* — mongrel): a cross-bred plant; the offspring of differing parents of the same or of different species.

HYBRID VIGOR (L. *hybrida* — mongrel, L. *vigere* — to be strong): increased vigor resulting from hybridization.

HYBRIDIZATION (L. *hybrida* — mongrel): the act of breeding differing parents.

HYDROLYSIS (Gr. *hydor* — water, and Gr. *luo* — dissolve): transformation of a compound into simpler compounds, involving the union of water.

HYDROPHYTE (Gr. *hydor* — water, and Gr. *phyton* — plant): a plant which lives in water or exceedingly wet soil.

HYDROTROPISM (Gr. *hydor* — water, and Gr. *trope* — turn): a growth movement in response to the stimulus of water.

HYGROSCOPIC WATER (Gr. *hygron* — moisture, and Gr. *skopeo* — look, observe): water directly surrounding and penetrating soil particles and retained by adsorption forces.

HYPERTROPHY (Gr. *hyper* — over, and Gr. *trophe* — food): an abnormally large growth, resulting usually from a disease.

HYPHA (Gr. *hyphe* — web): a fungous filament.

HYPOCOTYL (Gr. *hypo* — under, *kotyle* — cup): the portion of an embryo axis below the attachment of the cotyledons.

HYPOGYNY (Gr. *hypo* — under, and Gr. *gyne* — female): a condition in which the ovary surmounts a receptacle, and in which the sepals, petals, and stamens are attached below the ovary.

IGNEOUS ROCK (L. *ignis* — fire): rocks formed as a result of the solidification of molten matter.

IMBIBITION (L. *imbibere* — drink in): the process by which solid (chiefly organic) materials absorb water and swell.

IMMUNITY (L. *immunis* — exempt): resistance to the development of a disease.

IMPERFECT FLOWER (L. *imperfectus* — not perfect, L. *flos* — flower): a flower which bears stamens or carpels but not both.

INCLUSION (L. *includere* — to shut in): a non-living structure within the cytoplasm.

INCOMPLETE FLOWER: a flower which lacks one or more of the four kinds of flower organs. See complete flower.

INDEHISCENT (L. *in* — not, and L. *dehiscere* — split open): referring to a fruit which does not split open along regular seams or lines.

INDEPENDENT ASSORTMENT: the hereditary determiners which come together in one generation may separate and combine in various ways in the next generation.

INFLORESCENCE (L. *inflorescere* — to begin to blossom): a flower cluster.

INNER BARK: a name for the phloem and cortex of bark.

INORGANIC COMPOUND: a substance which is not a hydrocarbon or one of its derivatives.

INSECTIVOROUS (L, *insecare* — cut in, and L. *voro*): insect-eating.

INTEGUMENT (L. *integumentum* — covering): the coat of an ovule.

INTERNODE (L. *inter* — between, and L. *nodus* — knot): the length of stem between two successive nodes.

INULIN (Gr. *helenion* — basket): a white, complex carbohydrate very similar to starch.

INVERTASE (L. *invertere* — turn in or over): the enzyme which hydrolyzes cane sugar into glucose and fructose (fruit sugar).

ION (Gr. *ienai* — to go): an electrified particle formed by the breakdown of a molecule of certain substances (electrolytes).

IRRITABILITY (L. *irrito* — excite): the ability of living protoplasm to receive stimuli and respond to them.

ISOGAMETES (Gr. *isos* — equal, and Gr. *gamos* — marriage): gametes which are alike in size, structure, and often in behavior.

ISOGAMY (Gr. *isos* — equal, and Gr. *gamos* — marriage): sexual reproduction by isogametes.

LAMELLA (L. diminutive of *lamina* — a thin sheet): one of the constituent layers of a cell wall.

LATERAL BUD: an axillary bud.

LATEX (L. *latex* — juice): a milky fluid found in the tissues of certain plants.

LEAF: one of the lateral outgrowths of a stem, produced in succession by the growing point of a bud and having a bud in its axil.

LEAF AXIL (L. *axilla* — armpit): the upper angle between a leaf stalk and the stem from which it grows.

LEAF BUD: a bud which develops into a leafy shoot and does not produce flowers.

LEAF GAP: a break in the vascular cylinder, caused by the branching of vascular tissue from the cylinder into a petiole.

LEAF PRIMORDIUM (L. *primordium* — beginning): an outgrowth which develops from the growing point of a bud and which grows into a leaf.

LEAF SCAR: a scar left on a twig following the fall of a leaf.

LEAF TRACE: branches of the vascular tissues of a stem, extending out into leaves.

LEAFLET: one of the several blades of a compound leaf.

LEGUME (L. *legumen*, from L. *legere* — to gather): a simple, dry, dehiscent, one carpellate family splitting along two seams; a member of the legume family, the members of which have such fruits.

LENTICEL (L. *lens* — lentil): in woody stems, a pore in the bark through which exchange of gases occurs.

LEUCOPLAST(ID) (Gr. *leukos* — white, and Gr. *plastos* — formed): a colorless plastid involved in the formation of starch grains.

LICHEN (Gr. *leichen* — tree-moss): a symbiotic association of an alga and a fungus.

LIGNIFICATION (L. *lignum* — wood, and L. *facere* — make): impregnation of cell walls with lignin.

LIGNIN (L. *lignum* — wood): an organic substance (or group of substances) associated with cellulose in the cell walls, especially xylem, of many plants.

LINKAGE: the tendency for certain genes to remain together in inheritance.

LIPASE (Gr. *lipos* — fat): an enzyme which hydrolyzes fats to glycerol and fatty acids.

LIVERWORTS (Gr. *liparos* — fat, and AS. *wyrt* — herb, root): one of the classes of bryophytes.

LOBED (Gr. *lobos* — lobe of ear): divided by clefts, as a maple leaf.

LOCULE (L. *locus* — place): one of the cavities of an ovary.

MALTASE: an enzyme which hydrolyzes malt sugar (maltose) to grape sugar (glucose).

MATURATION (L. *maturatio* — hasten): process of becoming mature.

MECHANISM (Gr. *mechanao* — invent, contrive): a philosophical and biological viewpoint which holds that all activities of living organisms can be explained in terms of chemical and physical reactions.

MEGASPORES (Gr. *megas* — large, and Gr. *spora* — seed): a spore which in certain pteridophytes and in all seed plants grows into a female gametophyte.

MEIOSIS (Gr. *meioun* — make smaller): reduction division; the process by means of which chromosome numbers are reduced one half.

MERISTEM (Gr. *meristos* — divided): a mass of embryonic cells.

MERISTEMATIC (**EMBRYONIC**) **TISSUE**: a tissue the cells of which are capable of frequent division and which thus are responsible for the first phase of growth.

MESOCARP (Gr. *mesos* — middle, and Gr. *karpos* — fruit): middle layer of a fruit wall.

MESOPHYLL (Gr. *mesos* — middle, and Gr. *phyllon* — leaf): the leaf tissues between the epidermal layers.

MESOPHYTES (Gr. *mesos* — middle, and Gr. *phyton* — plant): plants which are intermediate between hydrophytes and xerophytes — that is, which grow in soils containing moderate amounts of moisture.

METABOLISM (Gr. *meta* — beyond, after, and Gr. *ballein* — throw): the sum total of the chemical transformations occurring in the body of a living organism.

METAPHASE (Gr. *meta* — after, and Gr. *phasis* — appearance): the stage in mitosis at which the chromosomes lie at the equator of the spindle.

MICROPYLE (Gr. *mikros* — small, and Gr. *pyle* — gate): the minute opening in the integument of an ovule, through which a pollen tube grows to reach the embryo sac.

MICROSPORES (Gr. *mikros* — small, and Gr. *spora* — seed): a spore which in certain pteridophytes and in all spermatophytes grows into a male gametophyte; in seed plants, a microspore is the young pollen grain.

MIDDLE LAMELLA (L. *lamina* — plate): the middle cell wall layer, composed chiefly of calcium pectate.

MITOCHONDRIA (Gr. *mito* — thread, and Gr. *chondros* — cartilage): granular or rod-shaped cytoplasmic structures, some of which are apparently plastid-formers.

MITOSIS (Gr. *mitos* — thread): a process of nuclear division involving the formation of a spindle and the formation and splitting of chromosomes.

MIXED BUD: a bud which produces both flowers and vegetative shoots.

MOLECULE (L. *moles* — mass): a unit of matter; the smallest particles of a chemical compound with the characteristic properties of the compound; a molecule is composed of atoms.

MONOCOTYLEDONS (Gr. *monos* — one, and Gr. *kotyledon* — cup-like hollow): a class of angiosperms with flower parts commonly in threes and a single cotyledon per seed.

MONOECIOUS (Gr. *monos* — one, and Gr. *oikos* — house): having staminate and pistillate flowers or male and female sex organs on the same plant.

MONOHYBRID CROSS (Gr. *monos* — one, and L. *hybrida* — mongrel): a cross between parents differing in a single character.

MORPHOLOGY · (Gr. *morphe* — form, structure, and Gr. *logos* — history, account): the study of the form and structure of organisms.

MOSSES (L. *muscus* — moss): a class of bryophytes.

MOTHER CELL: a cell which through cell division gives rise to other cells (daughter cells).

MULTIPLE FRUIT (L. *multus* — much, and L. *fructus* — fruit): a cluster of matured ovaries produced by separate flowers.

MUTATION (L. *mutare* — change): a sudden, heritable change produced in the offspring of a parent organism as a result of an alteration in a gene or chromosome; also, the process by which such changes occur.

MYCELIUM (Gr. *mykes* — mushroom): the mass of hyphae forming the body of a fungus.

NAKED BUD: a bud which is not protected by bud scales.

NATURAL PRESERVATIVES: preservative substances such as tannins and resins which occur naturally in woods and which tend to reduce disintegration by fungi and insects.

NATURAL (SELF) PRUNING: the natural dropping off of the branches and twigs of woody plants.

NATURAL SELECTION: the process which tends to cause "survival of the fittest" (survival of the organisms with the most advantageous variations for a given region); an important feature of Darwin's theory of the cause of evolution.

NECK: the tapering portion of an archegonium; a sperm enters an archegonium through a canal extending lengthwise through the neck.

NECTARY (Gr. *nektar* — drink of the gods): a floral gland which secretes nectar, a sweetish liquid which insects obtain from flowers.

NET VENATION (L. *vena* — vein): a scheme of vein arrangement in leaves, in which the veins branch frequently, forming a network.

NITRIFICATION (L. *nitrum* — saltpeter, and L. *facere* — make): the conversion of ammonia and ammonium compounds into nitrites and nitrates.

NITRIFYING BACTERIA: bacteria which carry on nitrification.

NITROGEN-FIXING BACTERIA: bacteria which live in the soil or in the roots of higher plants and which convert atmospheric, gaseous nitrogen into nitrogen compounds in the soil or in plant roots.

NODE (L. *nodus* — knot): a point on a stem from which a leaf and bud arise.

NODULE (L. *nodus* — knot): on the roots of certain plants, a swelling within which nitrogen-fixing bacteria live.

NUCLEAR MEMBRANE (L. *nucleus* — nut, and L. *membrana* — skin): a membrane which separates nuclear contents from the cytoplasm.

NUCLEAR SAP (L. *nucleus* — nut): the liquid present within a living nucleus.

NUCLEOLUS (diminutive of L. *nucleus* — nut): a small, usually spherical body found within the nucleus in most kinds of cells.

NUCLEUS (L. *nucleus* — nut): a usually spherical or ovoid body found in the protoplasm of most cells and considered as a directive center of many protoplasmic activities, including the transmission of hereditary characteristics.

NUT (L. *nux* - - nut): an indehiscent, dry, one-seeded, hard-walled fruit, produced from a compound ovary.

OLERICULTURE (L. *olus* — pot herb): the science of vegetable culture.

ONTOGENY (Gr. *on* — being, and Gr. *genesis* — origin): the life history, or development of an individual, as opposed to that of the race.

OOGONIUM (Gr. *oon* — egg, and Gr. *gonos* — offspring): the female sex organ in thallophytes.

OPPOSITE: bearing two leaves or two buds at a node.

ORDER: a category in the classification of plants, ranking between a family and a class; an order is composed of families.

ORGAN: one of the major parts of a plant body — leaf, stem, or root.

ORGANIC COMPOUND: a compound containing carbon.

OSMOSIS (Gr. *osmos* — push): the diffusion of a liquid (water) through a differential membrane.

OSMOTIC CONCENTRATION: the concentration of osmotically active solutes in a solution.

OSMOTIC PRESSURE: the maximum pressure which can be developed in a solution which is separated from pure water by a rigid membrane permeable only to water.

OUTER BARK: the cork tissue of woody stems and roots.

OVARY (L. *ovum* — egg): the basal, enlarged portion of a pistil, within which seeds develop.

PALEOBOTANY (Gr. *palaios* — ancient, and Gr. *botane* — plant): the science of the plant life of past geological ages.

PALMATELY VEINED (L. *palma* — palm of the hand): a type of net-venation in which the main veins of the leaf blade branch out from the apex of the petiole like the fingers of a hand.

PARALLEL EVOLUTION (Gr. *parallelos* — beside each other; L. *evolutio* — unrolling): evolution in a similar direction in different groups of organisms.

PARALLEL VENATION (Gr. *parallelos* — beside each other; L. *vena* — vein): a type of leaf venation, in which the principal veins are parallel to each other and to the longitudinal axis of the leaf.

PARASITE (Gr. *para* — beside, and Gr. *sitos* — food; literally, beside the table of another): a heterotrophic organism which derives its food from the living tissues of another organism.

PARENCHYMA (Gr. *parenchein* — to pour in beside): a tissue composed of thin-walled, often isodiametric cells, which often store food and usually retain embryonic potentialities.

PARTHENOCARPY (Gr. *partheno* — virgin, and Gr. *karpos* — fruit): the development of a fruit without pollination.

PARTHENOGENESIS (Gr. *partheno* — virgin, and Gr. *genesis* — beginning): the development of an egg into a new individual without fertilization by a sperm.

PATHOGEN (Gr. *pathos* — suffering, disease, and Gr. *genesis* — origin): an organism which causes a disease.

PATHOLOGY (Gr. *pathos* — suffering, disease, and Gr. *logos* — account, history): the study of diseases and their treatment.

PEDICEL (L. *pediculus* — little foot): the stalk of an individual flower of an inflorescence.

PEDUNCLE (L. *pedunculus*, a form of pediculus — little foot): the stalk of a solitary flower, or the main stalk of an inflorescence.

PERENNIAL (L. *per* — through, and L. *annus* — year): a plant which lives through several to many years.

PERFECT FLOWER (L. *perfectus* — finished, perfect; L. *flos* — flower): a flower which bears both stamens and carpels.

PERIANTH (Gr. *peri* — around, and Gr. *anthos* — flower): the floral envelope — i.e., calyx, and corolla.

PERICARP (Gr. *peri* — around, and Gr. *karpos* — fruit): the wall of a ripened ovary (fruit).

PERICYCLE (Gr. *peri* — around, and Gr. *kyklos* — ring, circle): in roots and stems, a layer (or layers) of cells immediately outside the phloem and inside the endodermis; branch roots develop from the pericycle.

PERIGYNY (Gr. *peri* — around, and Gr. *gyne* — female): a condition in flowers, in which the petals and stamens are usually fused with the calyx and in which the pistil is seated in a concave receptacle.

PERISTOME (Gr. *peri* — around, and Gr. *stoma* — mouth): a ring of teeth surrounding the opening of a moss capsule and by its hygroscopic movements scattering the spores.

PERMEABLE (L. *permeare* — to go, pass): capable of being passed through.

PETAL (Gr. *petalon* — a leaf): one of the divisions of a corolla.

PETIOLE (L. *petiolus* — a little foot or stalk): a leaf stalk.

PHAEOPHYCEAE (Gr. *phaeo* — brownish, and Gr. *phykos* — seaweed): the brown algae.

PHENOTYPE (Gr. *phanein* — show, and Gr. *typos* — model, type): referring to the external, visible appearance of an organism.

PHLOEM (Gr. *phloos* — bark): a conducting tissue, consisting principally of sieve tubes and companion cells; the chief function of phloem is food conduction.

PHOTOSYNTHESIS (Gr. *photos* — light, Gr. *syn* — together, and Gr. *thesis* — setting, arrangement): the manufacture of carbohydrate food from carbon dioxide and water in the presence of chlorophyll, utilizing light energy, and releasing oxygen.

PHOTOTROPISM (Gr. *photos* — light, and Gr. *trope* — turn): a growth movement induced by the stimulus of light.

PHYCOMYCETES (Gr. *phykos* — seaweed, and Gr. *mykes* — fungus): the algal fungi.

PHYLOGENY (Gr. *phylon* — tribe, and Gr. *genesis* — beginning): the development of a race of related individuals.

PHYSIOLOGICAL DISEASE: a non-parasitic disease resulting from a physiological disturbance.

PHYSIOLOGY (Gr. *physis* — nature, and Gr. *logos* — account, history): the science of the functions and activities of living organisms.

PILEUS (L. *pileus* — cap): the umbrella-like cap of a mushroom.

PINNA (L. *pinna* — feather): a leaflet of a fern leaf.

PINNATELY VEINED (L. *pinna* — feather, and L. *vena* — vein): a type of net venation in which the secondary veins branch out in parallel fashion from the single midrib of a leaf blade.

PISTIL (L. *pistillum* — pestle): the ovule-producing part of a flower, consisting of a single carpel (simple pistil) or of two or more partly or wholly fused carpels (compound pistil).

PISTILLATE FLOWER (L. *pistillum* — pestle, and L. *flos* — flower): a flower which bears a pistil but no stamens.

PITH (AS. *pitha* — pith): the spongy parenchyma tissue occupying the central portion of a stem within the vascular tissues.

PITH RAYS: primary bands of parenchyma cells extending from the pith to the pericycle in herbaceous stems.

PLACENTA (L. *placenta* – cake): a small mass of ovary tissue to which a seed stalk is attached.

PLACENTATION (L. *placenta* — cake): the arrangement of placentae within an ovary.

PLANKTON (Gr. *planktos* — wandering): free-swimming or floating aquatic organisms.

PLASMA MEMBRANE: see cytoplasmic membrane.

PLASMODESMA (Gr. *plasma* — formed, and Gr. *desma* — bond): protoplasmic connections between cells.

PLASMOLYSIS (Gr. *plasma* — formed, and Gr. *luo* — dissolve): shrinkage of protoplasm due to water loss.

PLASTID (Gr. *plastos* — formed): a cytoplasmic body involved in food synthesis, storage, etc.

POLES: the opposite ends of a mitotic spindle.

POLLEN GRAINS (L. *pollen* — dust, flour): the microspores and young male gametophytes of seed plants; minute structures which develop within anthers and which produce sperms.

POLLEN TUBE (L. *pollen* — dust, flour): a tube which is formed by a pollen grain and which transports sperms to the ovules.

POLLINATION (L. *pollen* — dust, flour): the transfer of pollen grains from a stamen to a stigma or ovule.

POME (L. *pomum* — a fruit): the apple-pear type of fruit, in which the true fruits (core) are surrounded by an enlarged fleshy calyx tube and receptacle.

POMOLOGY (L. *pomum* — a fruit, and Gr. *logos* — account, discourse): the science of fruit culture.

PRIMARY ROOT (L. *primus* — first): the root which develops directly from the radicle of an embryo.

PRIMARY TISSUE (L. *primus* — first, and Fr. *tisser* — weave): tissue developed by an apical meristem (tissue formed as a result of growth in length).

PRIMORDIUM (L. *primordium* — the beginning): the rudiment or beginning of a part or organ.

PROGRESSIVE EVOLUTION (L. *progressus* — forward movement): evolution from simple toward more complex and more highly specialized structure.

PROPHASE (Gr. *pro* — before, in front, and Gr. *phasis* — appearance): an early stage in plant mitosis in which the chromatin is organized into chromosomes and in which longitudinal splitting of the chromosomes begins.

PROTEINS (Gr. *proteios* — holding first place): complex, organic, nitrogenous substances built up from amino acids and constituting the major portion of the organic materials in living protoplasm.

PROTERANDRY (Gr. *proteros* — earlier, and Gr. *andros* — man): a condition in flowers in which the stamens mature and shed their pollen before the stigma of the same flower matures.

PROTEROGYNY (Gr. *proteros* — earlier, and Gr. *gyne* — woman): a condition in flowers in which the stigma matures and is pollinated by foreign pollen before the stamens of its own flower shed their pollen.

PROTHALLUS (PROTHALLIUM) (Gr. *pro* — before, and Gr. *thallos* — young shoot, frond): the gametophyte of a fern.

PROTONEMA (Gr. *protos* — first, and Gr. *nema* — thread): a branching filament forming an early stage in the gametophyte generation of a moss.

PROTOPLASM (Gr. *protos* — first, and Gr. *plasma* — formed): the living substance of plants and animals.

PROTOPLAST: the protoplasm of a single cell.

PTERIDOPHYTA (Gr. *pteris* — fern, and Gr. *phyton* — plant): a division of the plant kingdom including the ferns and fern allies.

PUTREFACTION (L. *putrere* — to be rotten, and L. *facere* — make): the anaerobic decomposition of organic substances, especially proteins, by micro-organisms.

RADIAL SECTION (L. *radius* — rod, spoke of a wheel): a section of a stem or root cut longitudinally on a radius.

RADIAL SYMMETRY (L. *radius* — rod, spoke of wheel; Gr. *syn* — together, and Gr. *metron* — a measure): a type of floral symmetry in which the flower may be separated into two approximately equal halves by a longitudinal cut in any plane passing through the center of the flower; that is, a flower built upon a wheel plan, rather than on a right and left plan. Example: rose, peony.

RADICLE (L. *radix* — root): the lower portion of the hypocotyl which grows into the primary root of a seedling; the root-primordium of a plant embryo.

RAY (L. *radius* — rod, spoke of a wheel): the corolla of a marginal or ray-flower of a composite inflorescence; a vascular ray.

RECEPTACLE (L. *recipere* — receive): the apex of a pedicel (or peduncle) to which the floral leaves are attached.

RECESSIVE (L. *recedere* — to go back, withdraw): one of a pair of contrasting characters, which is masked, when both are present, by the other, or dominant, character.

RESIN (L. *resina* — a resinous substance): a solid or semi-solid, often sticky, yellowish-

brownish organic plant product, insoluble in water, soluble in alcohol, used in the manufacture of varnishes, medicines, soaps, etc.

RESPIRATION (L. *re* — again, and L. *spiro* — breathe): a chemical oxidative process whereby living protoplasm breaks down certain organic substances with the release of energy which is used in various anabolic activities, movements, etc.

RETROGRESSIVE EVOLUTION (L. *retrogradare* — to go backward): evolution from a structurally complex or specialized condition toward a simpler, less specialized condition.

RHIZOID (Gr. *rhiza* — root, and Gr. *eidos* — form): in some thallophytes, bryophytes, and pteridophytes, hair-like appendages which penetrate the soil and absorb water and minerals.

RHIZOME (Gr. *rhiza* -- root): a horizontal, underground stem, commonly enlarged by the storage of food.

RHODOPHYCEAE (Gr. *rhodon* — rose, red, and Gr. *phykos* — sea-weed): the red algae.

RING-POROUS WOOD: wood in which the pores of one part of a growth ring are distinctly different in size or number from those in the other part of the ring.

ROOT CAP: a thimble-like mass of cells which fits over the apical meristem of a root and protects it.

RUNNER: a stem which grows horizontally over the surface of the soil and commonly develops new plants at its nodes.

RUN-OFF WATER: water which flows away without penetrating the soil.

SAC FUNGI: the ascomycetes, a class of fungi which bear spores in characteristic structures called asci.

SAMARA (L. *samara* — the fruit of the elm): a dry, indehiscent, one-seeded, winged fruit, such as that of elm or maple.

SAPROPHYTE (Gr. *sapros* — rotten, and Gr. *phyton* — plant): a heterotrophic plant which derives its food from non-living organic matter.

SAPWOOD: the young, physiologically active wood of a tree, consisting of the usually light-colored, outermost annual rings.

SCHIZOMYCETES (Gr. *schizo* — split, and Gr. *mykes* — fungus): the bacteria; the technical name refers to their characteristic method of reproduction by fission.

SCION (Fr. *scion* — sprout): a detached shoot used in grafting; the shoot which receives the scion is called the stock.

SCLERENCHYMA (Gr. *skleros* — hard, and *chymos* — juice): a strengthening tissue composed of thick-walled, elongated cells (fibers) or shorter cells (stone cells).

SECONDARY ROOT: a branch of a primary root.

SECONDARY TISSUES: tissues arising from a lateral or secondary meristem, such as the cambium or cork cambium, and increasing the diameter of a stem or root.

SEDIMENTARY ROCK (L. *sedimentum* — settling): rock formed by the hardening of substances settling out of water.

SEED: the characteristic reproductive structure of seed plants, consisting of an embryo, enclosed by a seed coat and often a food-storage tissue (endosperm).

SEED COAT: protective surface layer of a seed, formed from the integument of the ovule.

SEED SCARIFICATION: cutting or scratching a seed coat to facilitate the entry of water or oxygen.

SEGREGATION (L. *segregare* — to separate): the separation of hereditary determiners during reduction division; also, the separation of the visible characters controlled by these determiners.

SELECTION (L. *seligere* — select): the process of isolating and preserving certain individuals or characters from a group of individuals or characters.

SELF-POLLINATION: the transfer of pollen from stamen to the stigma of the same flower or of another flower on the same plant.

SELF-STERILITY: a condition in which self-pollination cannot result in the formation of seeds.

SEMI-PERMEABLE (L. *semi* — half, partly, and L. *permeare* — go, pass): referring to a membrane which allows certain substances to pass through and prevents the passage of others; same as differentially permeable.

SEPALS (Gr. *skepe* — covering): the divisions of a calyx; the outermost floral leaves.

SERUM (L. *serum* — watery part): blood liquid which contains antibodies; such liquid is obtained from the blood of an animal which has had the disease, the antibodies for which being present in the liquid.

SESSILE (L. *sessilis* — low, dwarf): lacking a stalk.

SEXUAL (L. *sexus* — sex): referring to a type of reproduction involving the fusion of paired sex cells (gametes), derived from the same parents or from two parents.

SHOOT: a stem with its leaves.

SHRUB: a woody plant with several stems arising from the root system.

SIEVE TUBE: a tube consisting of an end-to-end series of living phloem cells with perforated end walls.

SOFTWOOD: the wood of gymnosperms; a wood lacking wood fibers.

SOIL SOLUTION: the water with dissolved substances in the soil.

SOL: a liquid colloidal system.

SOLUTE: a substance in solution.

SORUS (Gr. *soros* — heap): a cluster of sporangia on a fern sporophyte.

SPECIES (L. *species* — form, kind, quality): the usually smallest unit in the classification of organisms; a group of individuals of the same ancestry, of similar structure and behavior, and of relative stability in nature. Example: bur oak, sugar pine.

SPERM (Gr. *sperma* — seed): male gamete, or sex-cell.

SPERMAGONIUM (Gr. *sperma* — seed, and Gr. *gonos* — offspring): flask-shaped structure on barberry leaf bearing spermatia of the wheat-rust fungus.

SPERMATIUM (Gr. *sperma* — seed): in the rusts, cells which are produced in spermagonia and which fuse with cells of opposite strain, following which aecia develop; also, the male gamete of red algae.

SPERMATOPHYTA (Gr. *sperma* — seed, and Gr. *phyton* — plant): the seed plants — angiosperms and gymnosperms.

SPIKE (L. *spica* — ear of grain): an inflorescence in which the sessile flowers are arranged along a longitudinal axis, with the oldest flowers at the base and youngest flowers at the apex of the stalk.

SPIKELET (L. *spica* — ear of grain): a unit of a grass inflorescence, consisting of one or more flowers and their bracts.

SPINDLE: the spindle-shaped mass of fibers formed during mitosis.

SPINDLE-FIBERS: fiber-like structures comprising the mitotic spindle and involved in the separation of the chromosome halves.

SPIREME (Gr. *speireme* — coil): the chromatin of a nucleus in the form of a continuous or segmented thread in the prophase of mitosis.

SPIRILLUM (L. *spira* — coil): a curved or spiral-shaped bacterium.

SPORANGIOPHORE (Gr. *spora* — seed, Gr. *angeion* — receptacle, and Gr. *phoros* — bearer): a stalk which bears a spore-case.

SPORANGIUM (Gr. *spora* — seed, and Gr. *angeion* — receptacle): a spore-case.

SPORES (Gr. *spora* — seed): an asexual reproductive structure, commonly unicellular.

SPORE MOTHER-CELL: a cell which by cell divisions produces typically four spores.

SPOROPHORE (Gr. *spora* — seed, and Gr. *phoros* — bearer): a spore-bearing structure, for example, a mushroom.

SPOROPHYLL (Gr. *spora* — seed, and Gr. *phyllon* — leaf): a spore-bearing leaf.

SPOROPHYTE (Gr. *spora* — seed, and Gr. *phyton* — plant): the spore-producing phase in alternation of generations, with the diploid chromosome number.

SPRINGWOOD: the portion of an annual ring formed in the early part of a growing season and consisting typically of cells which are larger than those formed later in the season.

STAMEN (L. *stamen* — thread, fiber): a pollen-producing organ.

STAMINATE FLOWER (L. *stamen* — thread, and L. *flos* — flower): a flower which bears stamens but no carpels.

STARCH (Gr. *starke* — strength, starch): a white, complex, water-insoluble carbohydrate, a common storage food in many plants.

STELE (Gr. *stele* — post, column): a collective name for the vascular and closely associated tissues in stems and roots: xylem, phloem, pericycle and endodermis.

STIGMA (Gr. *stigma* — spot, mark): the part of a pistil, usually the apex, which receives pollen and upon which pollen grains germinate.

STIPE (L. *stipes* — post, branch): a stalk, as the stalk of a mushroom.

STIPULE (L. *stipula* — stalk, stem): one of a pair of small appendages borne at the base of a leaf in many species of plants.

STOCK: in a graft, the basal portion of a stem, upon which a scion is grafted; also, a stem, or a race or group of genetically similar organisms.

STOLON (L. *stolo* — shoot): a runner.

STOMA (Gr. *stoma* — mouth): a pore, controlled by guard cells, in the epidermis of a stem or leaf.

STONE CELLS: thick-walled, isodiametric, strengthening cells of sclerenchyma tissue.

STRATA (L. *stratum* — spread, layer): layers of sedimentary rock.

STROBILUS (Gr. *strobilos* — a cone): a cone-like collection of sporophylls.

STYLE (Gr. *stylos* — pillar): in flowers, a cylindrical structure which rises from the top of an ovary and through which pollen tubes grow.

SUBERIN (L. *suber* — cork): a waxy, waterproof substance deposited in the walls of certain types of cells, such as cork cells.

SUBERIZATION (L. *suber* — cork): the deposition of suberin in a cell wall.

SUBTERRANEAN STEM (L. *sub* — under, and L. *terra* — land, earth): a stem which grows beneath the surface of the soil.

SUMMERWOOD: the portion of an annual ring of wood formed late in the growing season and consisting of cells smaller than those of springwood.

SYMBIOSIS (Gr. *syn* — with, and Gr. *bios* — life): an association of two or more kinds of living organisms, often resulting in mutual benefits.

SYNERGIDS (Gr. *synergos* — working together): two small cells lying near the egg at the micropylar end of the embryo sac in an ovule.

TANGENTIAL SECTION (L. *tangere* — to touch): a section of a cylindrical organ (e.g., a stem), cut lengthwise and at right angles to a radius of the organ.

TANNIN: a bitter, astringent, organic substance found in certain plant tissues, such as bark, heartwood, etc.

TAP ROOT SYSTEM: a root system in which there is a primary root distinctly larger and more conspicuous than any of its branches. Contrast diffuse (fibrous) root system.

TAXONOMY (Gr. *taxis* — arrangement): the science of the classification and arrangement, according to relationships, of living organisms.

TELIOSPORE (Gr. *telos* — end, completion, and Gr. *spora* — seed): the winter spore of a rust.

TELOPHASE (Gr. *telos* — end, completion; Gr. *phasis* — appearance): the final stage in mitosis in which the daughter nuclei are organized from the two sets of chromosomes, and processes leading to the formation of a new cell wall separating the daughter nuclei are initiated.

TENDRIL (L. *tendere* — to stretch out): a slender, coiling organ which aids in the support of plant stems; a tendril may be a modified stem, leaf, leaflet, or stipule.

TERMINAL (L. *terminus* — limit, end): occurring at the apex of an organ, as a terminal bud.

TETRAD (Gr. *tetra* — four): a group of four cells (usually spores) produced by two divisions of a mother cell.

TETRASPORES: the spores of a tetrad.

THALLOPHYTA (Gr. *thallos* — young shoot, and Gr. *phyton* — plant): the lowest of the plant divisions, comprising the algae and fungi.

THALLUS (Gr. *thallos* — young shoot): a simple plant body, with relatively little cellular differentiation, characteristic of the Thallophyta.

THIGMOTROPISM (Gr. *thigma* — touch, and Gr. *trope* — turn): growth movement in response to a contact stimulus.

TISSUE (Fr. *tisser* — to weave): an aggregation of cells, usually of similar structure, which perform the same or related functions.

TOXIN (Gr. *toxikon* — arrow poison): poisonous secretion of a living organism.

TRACHEID (Gr. *trachys* — rough, rugged): a type of conducting and strengthening cell in xylem tissue, of elongated tapering form and with pitted walls.

TRANSLOCATION (L. *trans* — across, and L. *locare* — place): the movement of materials within a plant body; more specifically, the movement of foods and other organic materials within a plant body.

TRANSPIRATION (L. *trans* — across, and L. *spirare* — to breathe): the emission of water vapor from the aerial parts of plants, chiefly through the stomata.

TRANSVERSE SECTION (L. *trans* — across, and L. *vertere* — to turn): a section cut at right angles to a longitudinal axis.

TRAVERTINE (L. *Tibur* — an ancient Roman town): a type of calcium carbonate rock, some of which was formed by the secretion of carbonate from algae.

TREE: a woody, perennial plant with a single main stem (trunk) arising from the root system.

TROPISM (Gr. *trope* — turn): a bending movement of a cylindrical organ or other cylindrical structure, caused by differences in growth rate in different parts of the organ and induced by external stimuli.

TRYPSIN (Gr. *tryein* — rub down, digest): a protein-digesting enzyme.

TUBE NUCLEUS: one of the nuclei in a pollen tube, influencing the growth and behavior of the tube and not concerned in sexual fusion.

TUBER (L. *tuber* — lump, swelling): much enlarged, fleshy, underground stem, commonly borne at the end of a rhizome.

TURGIDITY (L. *turgere* — to swell): state of being plump or swollen as a result of water pressure.

TURGOR (L. *turgere* — to swell): state of turgidity in living cells.

TURGOR MOVEMENT (L. *turgere* — to swell): a movement resulting from a usually rather sudden change in the turgor of certain cells in an organ.

TURGOR PRESSURE: (L. *turgere* — to swell, and L. *pressura* — pressure): the actual pressure developed by the water within a turgid plant cell.

TWIG SCAR: a scar left by the falling away of a twig.

TWINER: a plant which climbs by the twining movement of its stems about a suitable support.

UNICELLULAR (L. *unus* — one, and L. *cella* — small room): one-celled, referring to an organism the entire body of which consists of a single cell.

UREDOSPORES (L. *urere* — burn, scorch, and Gr. *spora* — seed): the summer spores of a rust fungus.

VACCINE (L. *vacca* — cow): a substance composed of weakened or dead bacteria (or other pathogens) or their diluted toxins, injected into the body to induce immunity to the same kind of pathogen or its toxins.

VACUOLE (L. *vacuum* — vacuum): a cavity within the protoplasm containing a watery solution of sugars and other substances.

VARIATION (L. *varius* — various, different): in an organism, difference in structural or physiological characters from those typical or common in the species to which the organism belongs.

VASCULAR BUNDLE (L. *vas* — vessel): a strand of conducting and strengthening tissues (xylem and phloem) in a plant organ.

VASCULAR RAY (L. *vas* — vessel, and L. *radius* — rod, spoke of wheel): a ribbon-like aggregate of cells extending radially in stems through the xylem and often the phloem.

VASCULAR TISSUE (L. *vas* — vessel, and Fr. *tisser* — weave): conducting tissue; xylem and phloem.

VEGETATIVE ACTIVITIES (L. *vegere* — to be active): activities most directly concerned with growth and the maintenance of the individual, rather than with reproduction.

VEGETATIVE REPRODUCTION: reproduction by a root, stem, leaf, or some other primarily vegetative part of a plant body.

VEIN (L. *vena* — vein): one of the vascular bundles of a leaf.

VENATION (L. *vena* — vein): the arrangement of the vascular bundles in a leaf.

VENTER (L. *venter* — belly): the enlarged base of an archegonium within which an egg develops.

VESSEL (L. *vas* — vessel): a conducting tube in xylem tissue.

VIABILITY (L. *vita* — life): the ability to live and grow; applied usually to seeds and spores.

VIRUS (L. *virus* — poison): a parasitic pathogen capable of reproduction in a suitable host, ultra-microscopic in size, and recognizable only because of the visible effects produced in the infected host.

VITALISM (L. *vita* — life): the doctrine which holds that the phenomena of life are not expressible ultimately in terms of chemistry and physics but that they are associated with a vital force distinct from chemical and physical forces.

WATER TABLE: the upper limit of the standing water in the wholly saturated portion of the soil.

WHORL: a circle of parts, such as leaves.

WHORLED: having several parts arranged in a circle at the same level; commonly applied to the condition in which 3 or more leaves occur at a node.

WOODY PLANT: a plant with a large development of xylem.

XANTHOPHYLL (Gr. *xanthos* — yellow, and Gr. *phyllos* — leaf): a yellowish or brownish plant pigment commonly associated with chlorophyll.

XEROPHYTE (Gr. *xeros* — dry, and Gr. *phyton* — plant): a plant which grows in soils with scanty water supply, or in soils in which water is absorbed only with difficulty.

XYLEM (Gr. *xylon* — wood): a complex plant fibrovascular tissue, consisting of tracheids, vessels, wood fibers, ray cells, and parenchyma cells; wood.

ZOOSPORES (Gr. *zoion* — animal, and Gr. *spora* — seed): spores which are enabled to swim by the movements of cilia or flagella.

ZYGOTE (Gr. *zygon* — yoke): a fertilized egg; a cell arising from the fusion of gametes.

ZYMASE (Gr. *zyme* — ferment, yeast): an enzyme in yeasts and other plants which converts sugars into carbon dioxide and alcohol under anaerobic conditions.

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